AN ILLUSTRATION OF INHERITED CHARACTERISTICS IN SHEEP.

The black-faced Suffolk ram (at left) when crossed with the white-faced ewe of the horned Dorset breed (in middle) results in animals with speckled faces, of which the males are horned and the ewes hornless. Breeding from the latter leads to a type of ram (at right) combining the white face of the Dorset with the hornlessness of the Suffolk.

At left "Fife" Wheat—strong, but scanty yield. At right, wheat developed by crossing "Fife" Wheat of large cropping capacity.

The two pure strains of White Sweet Peas (at right and left) reverted, on crossing, to the Purple (shown in the middle).

(*See pages* 70 *to* 89.)

MENDELISM

BY

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Preface by Gaylord Wilshire

THAT society will change from its present Capitalistic form to a Socialistic form slowly by a series of minute variations has never appealed to me as probable. My own opinion has always been that we would finally come face to face with a great unemployed problem as the result of our inability to distribute our increased production, which is a result of our use of machinery, by our competitive wage system; that this crisis would be unexpected by the great majority of the people, and that it would be so acute that it would demand an immediate solution. The immensity of the unemployed army of workingmen would threaten the absolute destruction of society. The only method of meeting this crisis is to be found in the substitution of the co-operative system of distribution for the competitive system. No half steps will meet the emergency because they would not reduce the unemployed problem sufficiently to relieve the situation.

In other words, my theory of the change of society from Capitalism to Socialism is that it must take place *per saltum*. My scientific friends have all said that such a theory was against the Darwinian theory, that evolution necessarily proceeded slowly, step by step. Of course, I could

answer that what applied to biology did not necessarily apply to sociology, but nevertheless I had to admit that the so-called Darwinian objection must at least be considered.

I could also point out the fact that the transition from an egg to a chick was a very distinct mutation, and yet a perfectly natural evolution. That to all outward appearance the egg was just the same the day it was due to hatch as it was the day it was laid, but that nevertheless a change had been going on within the shell which was not visible to the eye, and which made possible the sudden transformation of an egg into a chicken. In the same way I declared and prophesied that society was undergoing an evolutionary development, that it was suddenly to break its shell of Capitalism and merge at once into Socialism. I found in The Trust in America a significant sign that this world crisis was at hand, because the Trust means the capitalists were forced to merge in order to prevent the production of more machinery, because they had already produced all they could use. Any considerable cessation of the production of *new* machinery means the immediate development of a great unemployed problem, therefore the Trust was a significant sign of the approach of this great social problem. If it had not been for the destruction of property by the various wars which have taken place in the last ten years, the Capitalistic

shell would to-day be very badly cracked. It is possible a war between Germany and England, or one between Japan and the United States, may again defer the breaking of the shell, but ultimately it seems to me inevitable that the transition from Capitalism to Socialism must come, and that when it does come it will come *per saltum*. As a final clincher to the argument for mutation in biology, the recent development of our knowledge regarding the law of Mendel is of intense interest. As Professor Jacques Loeb of Berkeley, California, writes me:

"If the Mendelian theory is generally applicable, as I believe it is, the logical outcome is that evolution takes place by mutation only. Almost every day brings new evidence in support of Mendel's theory, and none against it. This theory has shown itself more fertile than any other which biology has ever produced, and the guarantee of its correctness lies in the fact that it is possible to predict results numerically. In this respect it differs radically from Darwin's hypotheses, which lack that element of numerical prediction and numerical verification."

If then all evolution proceeds by mutation I think the case is still strong for my declaring the change in society must proceed by mutation. The most interesting part of the Mendelian theory is that it is a mathematical one, and this is what

charms me regarding the theory of mutation in society. It, too, is a mathematical one. You can count up the number of machines and count up the number of men, and can prophesy the time almost exactly when Socialism must come in order to make a balance between production by machines and consumption by men.

Another interesting point regarding the Mendelian theory. Men can never be made all of the same mold if they are born with inherited characteristics which cannot be changed by environment. Socialism can not reduce us all to a dead level if Mr. Punnett is right.

Preface to Second Edition

LESS than two years have passed since the first edition of this little book appeared, yet so rapid has been the progress of Mendelian studies that part of what was then written is already out of date. Why the dwarf pea sprung from tall ancestors breeds true to dwarfness: why the progeny of a black and a white rabbit are in one case all black, and in another all of the wild grey color; why the 'pure' blue Andalusian fowl must ever remain a mongrel—these and other seeming paradoxes were clear two years ago. But why two white sweet peas should give a purple, and why two hairless stocks should revert to the hairy form—these were questions that were then unsolved. That experiment would give us the solution we were confident, and our confidence has been justified by the event. The sweet pea and the stock have yielded up their secret, and we are at last able to form a clear conception of the meaning of 'reversion.'

These recent discoveries have necessitated some re-writing and some additions. Mendel and his experiments stand where they always must stand, but the conception of synthesis has broken up, and the compound allelomorph is dead. Into their place comes the account of dihybridism in all its various aspects, and it is hoped that the diagrams

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added will assist the reader to grasp the unity which underlies this series of phenomena.

A short and popular essay like the present can give but little idea of the great body of facts already in existence. It would require a larger volume to do justice to the evidence, and to the devoted enthusiasm of the workers who in three continents have sought it out. Those who are interested may be referred to the forthcoming book of Mr. Bateson on Mendel's principles of heredity.

Meanwhile the work goes on. Each new riddle solved propounds fresh riddles, and strengthens the hope of their solution. As year follows year, and experiment succeeds experiment, there is forced upon us a sense of what it all may come to signify for ourselves, of the tremendous powers of control that a knowledge of heredity implies. To-day we are only at the beginning. The prologue is nearing completion; the drama is yet to be written—and played.

R. C. P.

February, 1907.

MENDELISM

"His humour was nothing but mutation."
—*Cymbeline.*

INTRODUCTORY.

It is the fortune of some great discoveries in natural knowledge to appear with the good-will and acclamation of all. So it has been with gravitation and radio-activity. It is the lot of others to stir up immediate animosity, causing men to judge of them rather through their passions than by their reason. More especially is this so where the religious beliefs and prejudices of mankind are concerned, as instance Galileo and Darwin. In either case the issue of the forward step is from the first clear to all according to their degree. But it may at times happen that a discovery of the first magnitude excites but little interest or comment. For the meaning of it is not at once apparent. Such has been the fortune of Gregor Mendel's great discovery in heredity, of which the story forms one of the most romantic chapters in the history of science. It is the aim of the following pages to give a brief account of Mendel's work with its more recent developments, and to touch upon some of the general consequences that flow from his experiments.

BIOGRAPHICAL.

Gregor Mendel was born in 1822, of Austro-Silesian peasants. When twenty-one years of age he entered a religious foundation at Brünn, and a few years later was ordained priest. Subsequently he studied the natural sciences for several years in Vienna (1851-53). He became interested in the problems of hybridization, and on his return to the cloister of Brünn commenced his classic experiments on the eating pea—*Pisum sativum.* The results appeared as a paper in the Proceedings of the Natural History Society of Brünn, under the title "Experiments in Plant Hybridization." Besides this paper Mendel contributed very little to biological literature. Nevertheless, we now know that he devoted much of his time to similar work on other plants. In a series of letters to Carl Nägeli, the botanist, he gives an account of his pea experiments, and also of others dealing with *Lychnis,* thistles, etc. Nägeli, however, like the rest of his contemporaries who knew of Mendel's work, was unable to appreciate the magnitude of the discovery. Perhaps Darwin alone could have valued Mendel's little pamphlet at its proper worth, and into his hands unfortunately it never fell.

The Abbot of Brünn, for such he afterwards became, was a man of wide and varied interests.

Besides his experiments on plants, he is known to have carried out others on bees, though the record of them would appear to have been lost. Meteorology was a hobby with him, and he contributed numerous observations on the subject to the Brünn Natural History Society. He was also much interested in sun-spots, and was for a time the manager of a bank. By the members of his cloister he was greatly liked and respected, though perhaps not altogether understood. He died of Bright's disease in 1884 at the age of 61.

EARLY NEGLECT OF MENDEL'S WORK.

For five-and-thirty years Mendel's work remained unknown. It had appeared at an unfavorable moment. Six years previously Darwin's views on the origin of species had been given to the world, and men of science were beginning eagerly to explore the new fields which he opened up. Hybridizers there had been before Darwin, but for lack of a central clue their results appeared as an inconclusive and disappointing tangle. Yet it was this very clue that Mendel's work supplied. With the advent of the "Origin of Species" men regarded as settled the question which the hybridizers had striven to answer, and directed their energies into other and more promising channels. Of late years doubts have been cast upon the all-sufficiency of natural selection in the production

of new species. A revival of interest in these matters, on the part of a few biologists, led in 1900 to the re-discovery of the principles of heredity which Mendel had clearly enunciated nearly forty years before. To gain an idea of the scope of these principles one cannot do better than turn to Mendel's own account of his experiments.

MENDEL'S EXPERIMENTS.

In the selection of a plant for experiment Mendel recognized that two conditions must be fulfilled. In the first place the plant must possess differentiating characters, and secondly, the hybrids must be protected from the influence of foreign pollen during the flowering period. In *Pisum sativum* Mendel found an almost ideal plant to work with. The separate flowers are self-fertilizing, whilst complications from insect-interference are practically non-existent. As is well known, there are numerous varieties of the eating-pea exhibiting characters to which they breed true. In some varieties the seed color is yellow, whilst in others it is green. In some varieties the seeds are round and smooth when ripe; in others they are wrinkled. Some peas have purple, others have pure white, flowers. Some peas, again, when grown under ordinary conditions, attain to a height of 6 to 7 feet, whilst others are dwarfs which do not exceed 1½ to 2 feet. Mendel selected a cer-

tain number of such differentiating characters, and investigated their inheritance *separately for each character.* Thus in one series of experiments he concentrated his attention on the heights of the plants. Crosses were made between tall and dwarf varieties, which previous experience had shown to come true to type with regard to these characters.* It mattered not which was the pollen-producing and which the seed-bearing plant. In every case the result was the same. Tall plants resulted from the cross. For this reason Mendel applied the terms *dominant* and *recessive* to the tall and dwarf habits, respectively. The next step was to collect the seeds thus formed and to sow them in the following year. When this was done it was found that both tall and dwarf plants appeared in the offspring. Each individual was either tall or dwarf, and no intermediate appeared. Thus in one series of experiments Mendel obtained 1,064 plants, of which 787 were tall and 277 were dwarfs. That is to say, the tall plants were almost three times as numerous as the dwarfs. In other words, the dominant and recessive characters occur in the second generation of hybrids (F_2) † in the proportion of 3 : 1.

* See note, p. 67.

† For convenience it is customary to denote the hybrids arising from a first cross by the letter F_1 (= 1st filial generation). The successive generations arising from this F_1 generation are denoted by the

In the following year the seeds of this generation (F_2) were sown as before. From the seeds of the dwarfs came only dwarfs, *i. e.*, the recessive character bred true. The tall plants, however, were not all of the same nature. Some of them produced seed which gave rise to tall plants only. Others, again, formed seed from which sprang both talls and dwarfs in the proportion of 3 : 1. The tall plants of the F_2 generation were of two kinds, viz., those which carried only the tall character, and those which carried both the tall and the dwarf characters. The former we may for the present call 'pure,' and the latter 'impure' dominants. Thus in one experiment plants were raised from the seeds of 100 tall plants of the F_2 generation. Of these 100 plants, 28 produced seed giving tall plants only, whilst 72 yielded seed which gave rise to both talls and dwarfs. Hence, of the 100 tall plants tested in the F_2 generation, 28 must have been pure for the tall character, whilst 72 must have been carrying the dwarf as well as the tall character. The former numbers, 28 and 72, do not make a very exact approximation to the ratio 1 : 2. The numbers, however, are small, and the proportion is greatly affected by a slight deficiency on either side. From a much larger num-

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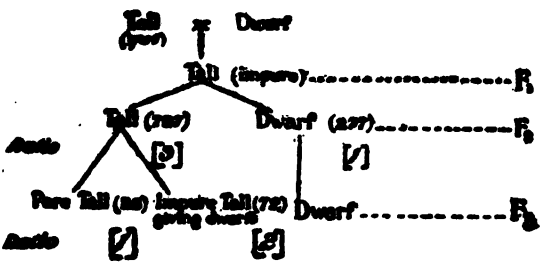
letters F_2, F_3, ... etc. The parents of the F_1 generation are called P_1 (=1st parental generation), the grandparents P_2, and so on.

ber of similar cases (between one and two thousand) Mendel found the ratio 1 : 2 borne out almost exactly. The dominants, therefore, which come in the F_2 generation are of two kinds—pure and impure. On the other hand, the dwarf recessives always breed true in whatever generation they appear. We may conveniently summarize the result of the experiments up to this stage in the following short table :



By breeding subsequent generations Mendel showed that the pure dominants and recessives always bred true, resembling in this way the original parents. The impure dominants, on the other hand, always gave dominants and recessives in the constant proportion of 3 : 1. Since the pure dominants are only half as numerous as the impure dominants, it follows that the impure dominant, on being selfed,* produces as offspring pure dominants, impure dominants, and recessives in

* See note, p. 67.

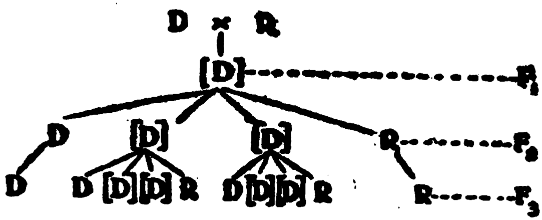
the proportion of 1 : 2 : 1. And this held good for all impure dominants, no matter in what generation they were bred. We have considered the case of one pair of characters only, but Mendel showed that the rule holds good for all the various pairs of differentiating characters studied by him. Wherever there occurs a pair of differentiating characters, of which one is dominant to the other, three possibilities exist:—there are recessives which always breed true to the recessive character: there are dominants which breed true to the dominant character, and are therefore pure: and thirdly, there are dominants which may be called impure, and which on self-fertilization (or inbreeding where the sexes are separate) give both dominant and recessive forms in the fixed proportion of three of the former to one of the latter.

GENERAL RESULTS OF THE EXPERIMENTS.

We are in a position now to make a general scheme to show the result of crossing individuals which each bear one of a pair of differentiating characters. If we denote the pure dominant by *D,* the impure dominant (which cannot be distinguished in appearance from the last) by [*D*], and the recessive by *R,* we may construct the following scheme of inheritance.

Such a scheme brings out clearly the points already referred to. When two pure strains, each

possessing one of a pair of differentiating characters, are crossed together, the resulting hybrids (F_1) all resemble the dominant parent.* When selfed, or bred among themselves, they give offspring (F_2), of which one quarter bear the reces-



sive and three quarters the dominant character. Of the latter, however, only a third are pure dominants, giving, when selfed, offspring in which the dominant character alone appears. The remaining two-thirds are impure dominants, which on selfing behave as the original F_1 hybrids, and yield pure dominants, impure dominants, and recessives in the proportions 1 : 2 : 1. And this is true of all impure dominants, no matter in which generation they occur. Both the 'extracted' pure dominants and the 'extracted' recessives, which are formed in any generation after a cross, breed

* The statement that the hybrid of the first generation cannot be distinguished from the dominant parent holds good for peas and many other forms of life, but, as will appear later (p. 29), it is not universally true.

true to the types of the original parents used in that cross.

EXPERIMENTS SUBSEQUENT TO MENDEL. (*a*) ON ANIMALS.

Mendel himself verified this principle of dominance for several characters in *Pisum*, finding round seeds dominant over wrinkled, colored seed-coats over white seed-coats, yellow seed-color over green, etc. Within the last few years the validity of the principle has been extended to numerous differentiating characters, both structural and physiological, in animals as well as plants.

To mention but a few cases: the colored coat of mice and rabbits is dominant over the unpigmented or 'albino' coat; the long 'Angora' fur found in some rabbits is recessive to the normal short fur; the 'rose' comb which occurs in certain breeds of poultry, such as Hamburgs or Wyandottes, behaves as a simple dominant towards the high-serrated 'single' comb characteristics of Leghorns, Andalusians and others.

(*b*) ON PLANTS.

Owing to the numbers in which they can be produced, and the ease with which they can be controlled, plants lend themselves more readily than animals to investigations of this nature. Of the many characters already investigated a few

only can be mentioned here. In wheat and barley the beardless have been shown to be dominant over the bearded forms. The dwarf or 'Cupid' variety of sweet pea, but a few inches in height, behaves as a recessive to the normal form. In maize the yellow-seeded variety is dominant over the white, and the so-called 'sugar' seed is recessive to the 'starch' seed. Among plants possessing colored and white varieties of flowers it has been shown that in general (*e. g., Datura*, stocks, sweet peas, etc.) the white forms are recessive to the colored. The hybrid resulting from the crossing of pure white with a colored form is always colored, though its actual color is not necessarily that of the colored parent. Thus a picotee sweet pea crossed with a white may give, not picotee, but purple.

WALTZING MICE.

The characters hitherto dwelt upon are concerned either with color or with what may be termed normal structural features. Leaving these we may turn for a moment to consider two most interesting cases, in which one of the pair of differentiating characters is in a markedly abnormal condition. Of the many breeds of fancy mice the Japanese 'waltzer' is one of the most distinct, and derives its name from a curious habit of vigorously circling round, sometimes for hours together, as if intent upon its own evasive tail. It has been shown

that these mice suffer from a malformation of the labyrinth of the ear, and it is of the greatest interest to find that this condition behaves as a single recessive to the normal state.

STERILE SWEET PEAS.

The second case alluded to occurs in the sweet pea. Sometimes there may be seen a few plants in a row, which, though to all appearances healthy and vigorous, set little or no seed. The reason is at once apparent when a flower is pulled to pieces. The anthers are sterile, containing only a little degenerate pollen, and the flower is consequently incapable of the normal self-fertilization which obtains among these plants. Such few pods as are formed presumably owe their origin to insect agency, for the female parts of the flower are perfectly normal, and readily set seed when pollenated from another plant. The F_1 hybrids so formed are all normal, showing that the fertile anther is dominant to the sterile. In the next generation (F_2) plants with sterile anthers reappear approximately in the proportion of 1 : 3 of the fertile, which is in accordance with expectation. This case of the sterile sweet pea is of great interest from its bearing on the problem of sex. Looked at from this standpoint, we have here a unisexual form, a female, which has suddenly arisen from the normal hermaphrodite form by functional suppression

of the male organs. It suggests that, in cases where the sexes are separate, this condition may have suddenly arisen from the hermaphrodite one. The story of sex, however, is too long and too complex for us to enter upon in this connection.

RESISTANCE TO DISEASE.

The characters we have just considered, though highly abnormal, are yet essentially structural. The Mendelian principles of heredity have, however, been demonstrated in the case of other characters of a less tangible nature. It has been shown, for instance, that the earlier ripening habit of Polish wheat is recessive to the later ripening habit of Rivett wheat. A still more interesting case occurs in the same species of plant. Certain forms of wheat are highly susceptible to the attacks of a fungus which causes 'rust,' whilst others are immune. It has recently been shown that immunity in this instance behaves as a recessive to the non-immune condition. When an immune and a non-immune strain are crossed together, the resulting hybrids are all susceptible to 'rust.' On self-fertilization such hybrids produce seed from which appear dominant 'rusty' and recessive immune plants in the expected ratio of 3 : 1. From this simple experiment the phrase 'resistance to disease' has acquired a more precise significance, and the wide field of research opened up in this

connection promises results of the utmost practical as well as theoretical importance. To the old question, "Who can bring a clean thing out of an unclean?" we are beginning to find an answer, nor is the answer the same as that once given by Job.

THEORETICAL DEDUCTIONS.

So far we have been concerned with the phenomenon of dominance as enunciated by Mendel, and borne out by subsequent experiments. We must now consider the theoretical results which Mendel deduced from his facts. It is a matter of common knowledge that in the majority of animals and plants the genesis of a new individual is the result of a sexual process, the essential feature of which consists in the union of a female cell, the egg or ovule, with a more minute male cell, the spermatozoon or pollen-grain. Such cells, both male and female, are termed *gametes,* and the cell formed by the fusion of a male with a female gamete is spoken of as a *zygote.* This unicellular zygote, by a process of repeated nuclear division, ultimately gives rise to the adult animal (or plant, as the case may be) with its contained germ-cells. The germ-cells, at first immature, subsequently ripen to form the gametes, thus completing the life-cycle. Since the gametes form the link connecting successive adult generations, the characters peculiar to the latter must be represented in the constitu-

tion of the former. In the case of a tall pea, some at least of the gametes formed, both male and female, must carry the tall character; for from an impure tall, three-quarters of the offspring are tall. And if the strain of tall peas is shown by experiment to be pure for that character, all the gametes must be carrying that character, and that alone. The union of two gametes in this case will result in a zygote having the tall character, to the formation of which each gamete has equally contributed.

HOMOZYGOTES AND HETEROZYGOTES.

Such a zygote is known as a *homozygote,* and when it comes to form gametes, these will all be similar as regards the character under consideration. A zygote formed by the union of two dissimilar gametes—*e. g.,* in the case of peas, where one bears the tall and the other the dwarf character—is termed a *heterozygote.* The heterozygote frequently exhibits the form of the pure dominant, from which it can only be distinguished by the test of breeding. That the recessive character is likewise carried is shown by the fact that when such heterozygotes are bred *inter se,* one-quarter of the offspring produced are recessive. It is only in this way that we can distinguish between the pure tall pea and the tall which bears the dwarf characters —between the pure 'rose' comb and the 'rose' comb which carries also the 'single' comb. There

are cases, however, in which the heterozygote does not resemble the dominant, but has a character peculiar to itself. Reference will be made to such cases later on.

UNIT-CHARACTERS.

These facts led Mendel to the conception of pairs of unit-characters,* of which either can be carried to any one gamete to the exclusion of the other. A fundamental property of the gamete is that it can bear either one of such a pair of characters, though not both. But the heterozygote is formed by the union of two dissimilar gametes, and consequently the cells of the individual into which it grows must contain both characters. To reconcile these statements it must be supposed that at some cell division in the formation of gametes a primitive germ-cell divides into two dissimilar portions. Instead of the dominant and recessive constituents passing in combination to the two daughter-cells, the whole of the dominant goes into one of these, and the whole of the recessive into the other. From this it follows that every gamete contains only one of such a pair of characters, *i. e.*, it is *pure* for that character. In other words, a simple heterozygote, such as we are considering, *produces gametes of two kinds, and produces them in equal numbers.*

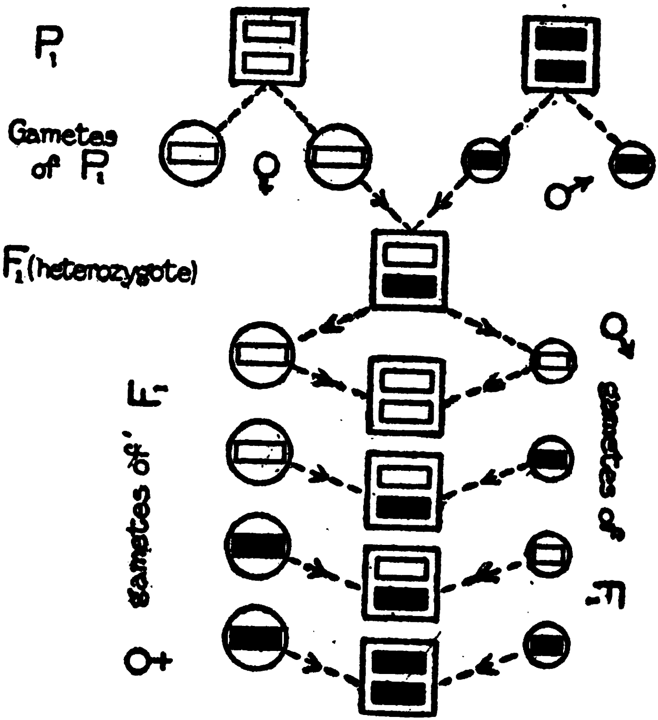
* Such pairs of unit-characters have since been termed *allelomorphic* pairs.

THE PRINCIPLE OF GAMETIC SEGREGATION.

The characters are said to *segregate* in the gametes. In this conception lies the simple explanation of the facts, that from the in-bred heterozygote come dominants and recessives in the proportion of 3 : 1, and that only one dominant in three is pure, the other two being heterozygotes.

The argument may perhaps be rendered clearer by reference to the accompanying scheme. The zygotes are here represented by squares, and the gametes by circles. Every zygotic cell, being formed by the fusion of two gametes, is a double structure, and contains two *factors** belonging to any given pair of characters. In the scheme these factors are represented by small rectangles, those corresponding to the recessive character being shown in black. The original parents (P_1) are supposed to be a pure tall and a pure dwarf, the latter being used as the pollen parent. All the ♀ female gametes must therefore bear only the tall, and all male the ♂ gametes only the dwarf, factor. Consequently only one type of plant can be formed in F_1, viz., a heterozygote containing the factors for both tallness and dwarfness. Owing to the com-

* By this term it is convenient to denote the physical basis for the unit-character which exists in the gamete. Tallness in the pea is a unit character, and is transmitted from one generation to another by the 'tall' factor in the gamete.



F_2 zygotes

plete dominance of the tall character these plants are indistinguishable from the tall parent. Since the factors are unsplittable, and since the gamete contains only half as many as the zygote, it is obvious that when these plants produce gametes they

must produce equal numbers of two sorts bearing the tall and dwarf factors respectively. Every ovule which bears the factor for tallness has an equal chance of being fertilised by a 'tall' or a 'dwarf' pollen-grain, and the 'tall' ovules will therefore give rise to equal numbers of homozygous and of heterozygous talls. Similarly the 'dwarf' ovules will give rise to equal numbers of heterozygous talls and of homozygous dwarfs. Hence, of every four zygotes in the F_2 generation, one will be homozygous for tallness, another homozygous for dwarfness, and the remaining two will be heterozygous in nature; though owing to the dominance of the tall character they will be indistinguishable in appearance from the pure talls. These we have already seen to be the proportions found by experiment, and the experimental results are to be regarded as the basis for the conception of unit-characters represented in the gamete by unsplittable factors which segregate from one another during the formation of the gametes.

A convenient system of notation is to denote the heterozygote by the letters *DR*, thus signifying that it gives off equal numbers of gametes bearing the dominant and recessive characters. On the same system the pure dominant and the pure recessive are represented by the terms *DD* and *RR* respectively. So far we have considered only the results obtained by in-breeding the heterozygotes.

HOMOZYGOTE BRED WITH HETEROZYGOTE.

The theory of gametic purity can be further tested by deducing from it the results which should follow from crossing the heterozygote with either of the homozygotes, and seeing how far such theoretical results accord with those obtained by experiment. When the heterozygote *DR* is crossed with the recessive *RR*, each dominant and each recessive gamete arising from the former can unite only with a recessive gamete formed by the latter. Consequently we should look for the production of equal numbers of zygotes of the constitution *DR* and *RR*. This is what actually happens on crossing a fowl having a single comb (*RR*) with one having a heterozygous 'rose' comb (*DR*). Half the offspring are pure recessives, and the other half are dominants which may be all proved to carry the 'single' character, *i.e.*, are heterozygotes. Similarly, when the heterozygote *DR* is crossed with the pure dominant form *DD*, we should, from theory, expect all the offspring to be dominant in form, and one half of them to be pure dominant. Here again experiment has borne out theory. The generalisation known as the principle of gametic segregation may be regarded as firmly established on the phenomena exhibited by plants and animals, when strains are crossed which possess pairs of differentiating characters.

Whether the principle applies universally or not can only be answered by subsequent experiment.

LIMITATIONS OF THE PHENOMENON OF DOMINANCE.

We have already seen that the heterozygote frequently resembles the dominant homozygote so closely that the two cannot be distinguished by inspection alone. This is by no means always the case. It sometimes happens that the heterozygote, whilst bearing a general resemblance to the dominant, differs from it sufficiently to enable us to tell the two apart. The white Leghorn breed of poultry is characterized by its white plumage. In this case white plumage is dominant to coloured, but the dominance is not quite perfect. When a white and a brown Leghorn are crossed together, all the resulting offspring are white,* but almost invariably have a few coloured feathers. The presence of these 'ticks' is the outward and visible sign of the heterozygous nature of the bird on which they occur. Such birds give off equal numbers of gametes bearing the white and coloured characters. This is easily tested by breeding them together. It is found that from such matings one quarter of the

* We know now that there also exist white chickens in which the whiteness behaves as a simple recessive to colour, and that these recessive whites are often indistinguishable in appearance from the dominant white. Not always does the plumage proclaim the fowl.

offspring are coloured recessives, whilst the remainder are pure white, or white with a few ticks. The heterozygote resembles the dominant form much more closely than it does the recessive. Though we may speak of dominance in such a case, it is necessary to remember the dominance is not perfect. This, however, makes no difference to the essential feature of Mendel's discovery, which is of course the segregation in the gametes of the factors corresponding to the dominant and recessive characters.

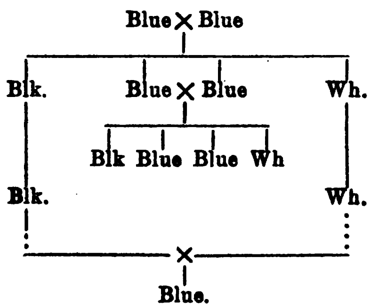
In addition to cases where the heterozygote differs slightly from the dominant homozygote, there are others in which it is quite distinct from either parent, and exhibits characters peculiar to itself.

THE CASE OF THE ANDALUSIAN FOWL.

The blue Andalusian fowl offers a very pretty instance of this. Breeders have long recognised the difficulty of obtaining a pure strain of this variety. No matter how carefully the blues are selected they always throw 'wasters' of two sorts, some pure black, and others of a peculiar white with black splashes. Careful breeding shews that, on the average, one half of the offspring from a pen of blue Andalusians come blue, one quarter black, and one quarter white. These proportions at once suggest that the blues are

heterozygotes. For we have already seen that the breeding of heterozygotes together results in one half of the total offspring coming heterozygotes. If this is so, it follows that the blacks and splashed whites are by nature homozygous, and consequently ought to breed true. Experiment has shewn that such is actually the case. Further, we should be led to expect heterozygous offspring from a union of the two different homozygotes. Here again the experimental result accords with the theory. When splashed black and white are bred together, all the offspring without exception are blue. Paradoxical as it may sound, the mating together of the black and the white 'wasters' gives a proportion of blue Andalusians twice as great as does the mating of blue with blue.* The black

* The following scheme, which may be compared with that on p. 17, will perhaps serve to render the above account easier to follow. The theory, of course, supposes that the blues are giving off white-bearing and black-bearing gametes in equal numbers, there being no such thing as a blue-bearing gamete. In the cross blue × blue the ♀ is producing equal numbers (2*n*) of 'white' and 'black' eggs—



and the white splashed are really the pure breeds; the 'pure' blue Andalusian is, and from its nature ever must be, a mongrel. From our point of view it is of interest as a case where the appearance of the heterozygote is quite unlike that of either of the homozygotes from whose union it springs. Yet, though there is no dominant and no recessive here, the essential feature of gametic purity could not be shewn more clearly.

DIHYBRIDISM.

The cases which we have hitherto considered, concern only a single pair of differentiating characters, that is to say, are cases of *monohybridism*. Where the original parents differ in two pairs of characters, the case is termed one of *dihybridism*. Mendel himself worked out several such instances, and found that the separate pairs, though obeying the same law of inheritance, were transmitted en-

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the ♂ equal numbers of 'white and 'black' sperms. A 'white' egg therefore, has an equal chance of being fertilized by a 'white' or 'black' sperm. When 'white' meets 'white' the result is white, and when 'black' meets 'black' the result is black. But when 'white' meets 'black' the result is blue. Hence $2n$ white eggs result in n white and n blue zygotes. Similarly, $2n$ 'black' eggs give rise to n black and n blue zygotes. Therefore, if the blue ♀ produce $4n$ eggs to the blue ♂, n of these will result in black zygotes, n in white zygotes, and $2n$ in blue zygotes. In other words, the black, white, and blue birds produced must be numerically in the proportion of 1 : 1 : 2. And this is the proportion found by experiment.

tirely independently of one another. When, for example, a tall yellow-seeded pea was crossed with a dwarf green-seeded one, the F_1 plants all exhibited the dominant character of each pair, and were tall yellows. In the next generation appear, as usual, talls and dwarfs in the ratio of 3:1, and also yellows and greens in the same ratio. If we suppose that there are 16 plants, it is clear that 12 of these will be tall, and that the other 4 will be dwarf. Now of every 4 talls, 3 will be yellows and the other green. Out of our 12 talls, therefore, 9 will be yellows and 3 will be green. Similarly, of the 4 dwarfs, 3 will be yellow and one will be green. Consequently, the F_2 generation arising from the cross will consist of 9 yellow talls, 3 green talls, 3 yellow dwarfs, and one dwarf green. In other words, there will be for every 16 plants a class of 9 shewing both dominants; two classes of 3 each shewing the dominant character of one pair and the recessive of the other; and one plant with both recessive characters. Mendel established by experiment that these were the proportions that actually occurred, a result which has been amply confirmed since his time for other plants as well as for animals. And the principle may be extended indefinitely for any number of pairs of characters.

NOVELTIES.

In the particular case which we have just con-

sidered, one of the original parents was homozygous for both the dominant, and the other for both the recessive, characters. Precisely the same result would have been attained had the original parents been a tall green and a dwarf yellow, instead of a tall yellow and a dwarf green. In either case the F_2 generation contains the two original parental types, and also two other combinations which we must regard as novelties. Where the two pairs of characters are as distinct as height and seed colour, the re-combination of characters which appears in the second generation is easy to follow. Sometimes, however, the reason of the appearance of a novelty is not at first sight so evident. The sweet pea known as the 'Painted Lady' is characterised by a bright pink standard and lighter wings. The colour here is due to the sap, and is dominant to the absence of such sap colour, in which case the flower is white. In the cream sweet pea there is no sap colour, the tint of the flower being due to the presence of yellow-colouring matter in the small bodies known as chromoplasts. Yellow chromoplasts are recessive to colourless ones. When a Painted Lady is crossed with a cream, the F_1 plants are all Painted Ladies. In the F_2 generation four classes occur, viz., Painted Ladies, cream Painted Ladies, *whites*, and creams; and these four classes occur in the ratio 9:3:3:1. The proportion in which the four forms

appear at once suggests the explanation of the case, which consists, of course, in being able to define the unit-characters involved. These must be—

(*a*) Red sap colour dominant to no sap colour;

(*b*) Colourless chromoplasts dominant to yellow.

The white, which appears as a novelty in 3 out of every 16 plants, is due to the combination of the character 'no sap colour' brought in by the cream with the character 'colourless chromoplasts' introduced by the Painted Lady. The apparent difficulty of the case, at first sight, lies in the fact that both of the unit-characters concern the same thing, viz., the visible flower-colour.

THE COMBS OF FOWLS.

A somewhat similar case in animals is presented by the behaviour of certain types of comb in fowls. Attention has already been drawn to two forms of comb found in different breeds of poultry, viz., to the high serrated 'single' comb characteristic of the Mediterranean races, such as the Leghorns and Andalusians, and to the flattened papillated 'rose' comb with its posterior pike that occurs in Wyandottes, White Dorkings, and others. As was mentioned above, the single and rose combs behave towards each other as simple recessive and dominant. A third type of comb is characteristic of the Indian game fowl. This, the so-called 'pea' comb,

is a rather low structure, possessing three well-marked ridges, of which the median is somewhat higher than the two lateral ones. Towards the single comb it behaves as a simple dominant. When, however, the rose and pea combs are crossed together, as for example by mating a White Dorking with an Indian game, an entirely new form of comb results. This is a broad flattened and somewhat corrugated structure, exhibiting neither the pike nor working of a rose comb, nor the three ridges of a pea. From its resemblance in shape to the half of a walnut, it may be called the 'walnut' comb. It occurs normally in a certain breed of fowls, the Malays. One of its peculiarities is that from certain portions of it grow out small bristle-like hairs. They occur on the posterior part of it, and often form a band running right across the comb at the junction of its posterior third with the remainder. The junction is usually marked also by a distinct transverse groove. The peculiar feathering of the comb is a feature not found in any of the other three types mentioned above. When these hybrid walnuts are bred together, four types of comb appear in the next generation, viz., walnuts, roses, peas, and *singles*, in the approximate ratio of 9:3:3:1. Here again the explanation of the case is at once suggested by this ratio. The two pairs of unit-characters concerned are (1) *Rose* which is dominant to *no*

rose, and (2) *Pea* which is dominant to *no pea.* Walnut is the form taken by the comb containing both of the dominant characters, and the single appears when the dominant of neither pair is present.

THE ALLELOMORPHIC PAIR.

The case of the fowl's comb is of great interest, because it throws fresh light upon the relations subsisting between the two members of an allelomorphic pair. Hitherto we have considered each member of such a pair as a definite entity, of such nature that the two are of equal value and interchangeable with one another, but not with the members of other pairs. We have looked upon the tall pea as tall because the factor for tallness is present, and we have regarded the conversion of a tall into a dwarf as involving the removal of the tall factor and its replacement by the dwarf factor. If two peas differ from one another solely in the pair of characters—tallness and dwarfness—we must suppose that for the characters in which they resemble one another they must contain identical factors, and therefore the same number of factors. For the one pair of characters in which they differ they each contain a factor, but a different one. On this view, then, the total number of factors must be considered to be the same in each plant. So long as the cases of dihybridism studied involved two widely different pairs of char-

acters, this view remained an adequate explanation of the facts. The case of the combs, however, presented a difficulty. It differed from previous cases, in that two pairs of characters both affected the same structure, the comb. Rose and pea are both dominant to single, and we cannot distinguish the single which is recessive to pea from that which is recessive to rose. Strip off 'roseness' from a rose and single remains. Strip off 'peaness' from a pea and single is left. Single is to be regarded as a common condition underlying both rose and pea, and it may become rose or pea according as the factor for either of these characters is added. The rose and the pea, therefore, each contain a factor more than the single, and the walnut contains two factors more.

So also with the many simple Mendelian cases already mentioned. The tall pea is a dwarf to which has been added the factor for tallness. Were our methods nice enough to dissect out and remove this factor from the gametes of the tall, we must suppose that they would produce only dwarfs. For the operation would allow of the manifestation of the dwarf character, which is always underlying the tall, and forming as it were the substructure necessary for the building of the tall.

THE PRESENCE AND ABSENCE HYPOTHESIS.

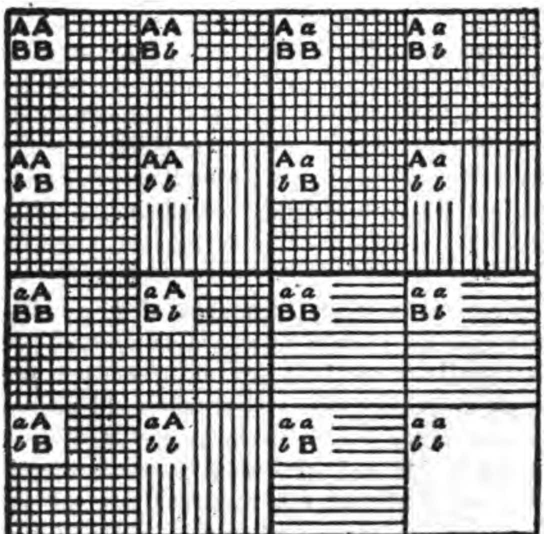
The Presence and Absence hypothesis, as we may term this view, offers a ready explanation of

one of the most widespread phenomena of heredity —the existence of characters in alternative parts. For there are but two relations into which the unsplittable unit-character can enter with the individual. It may be present, or it may be absent, and no third relation can be conceived. From this we are led to ask, whether the hypothesis can be brought into any simple relation with the phenomenon of dominance. Is dominance the outcome of the presence of the given factor, and recessiveness the condition implied by its absence? At present we can only say that such a point of view is not at variance with the great majority of the cases hitherto worked out. Whether the few instances which now seem contradictory will ultimately fall into line future work alone can decide.

DIHYBRIDISM AGAIN.

Returning now to the subject of dihybridism, we may briefly recapitulate in a generalised form the main features of the phenomenon before passing on to consider some special cases; and this may be conveniently done with the help of the diagram following. *Aa* and *Bb* denote two pairs of unit-characters, such that *A* is dominant to *a* and *B* to *b*. If we suppose one of the original parents to have been homozygous for *A* and *B*, and the other for *a* and *b*, we must represent them as *AABB* and *aabb* respectively. The constitution of the F_1 in-

dividual must therefore be *ABab*, and since it is heterozygous for the *Aa* pair it will give in F_2, $AA + 2\,Aa + aa$. This is denoted by the four large squares of the diagram. Again, since the F_1 individual is heterozygous for the *Bb* pair, the F_2 generation will be of the form $BB + 2Bb + bb$ for this pair of characters. This is represented in the diagram by dividing up each of the 4 orig-



inal squares into 4 again. Of the 16 squares resulting it will be noticed that:—

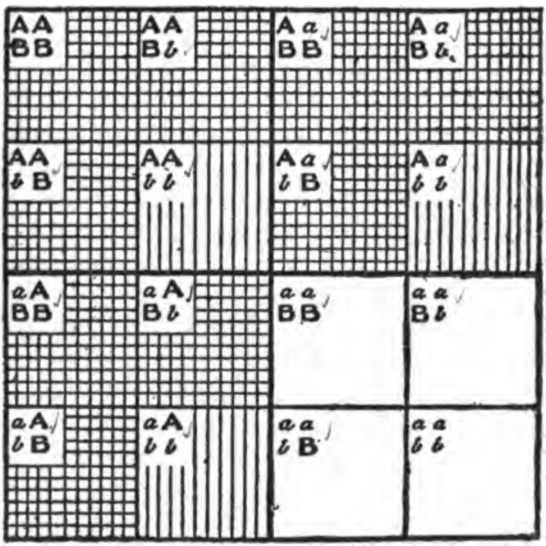
9 contain both A and B,
3 " A but not B,
3 " B but not A,
1 " neither A nor B.

And this is the 9:3:3:1 ratio which we have already met with in several cases of dihybridism. Further, it may be pointed out that of the 16 zygotes only 4 are homozygous for both of the unit-characters contained. These are represented by the 4 squares on the diagonal starting at the left top corner of the diagram, and one of them belongs to each of the four classes represented in the 9:3:3:1 ratio. Hence, the chance of an F_2 zygote, which contains both dominants, breeding true is 1 in 9, and of an F_2 zygote containing one dominant is 1 in 3. The F_2 generation, in a case of dihybridism, consists of four types, viz., the original parents and two new ones. Of each of these four types a certain definite proportion is fixed in this generation, and will afterwards breed true without any further selection. It is hardly necessary to point out the very great importance of this fact to those who are endeavoring to raise new and stable varieties by the method of cross-breeding.

MASKED CHARACTERS.

Cases of dihybridism are known in which apparent complications are produced by the interactions between the two pairs of factors. Experi-

ment has shewn that the wild grey colour in rabbits is dominant to black, and also that both grey and black are dominant to albino. When a rabbit of the wild grey colour is crossed with an albino, the offspring are all grey. On being bred together, these F_1 grey animals give in certain cases greys, blacks, and albinos in the proportion of 9:3:4. The explanation is as follows: The two pairs of characters concerned are (1) pigmentation (*A*)



dominant to absence of pigmentation or albinism (*a*), and (2) greyness (*B*) dominant to black-

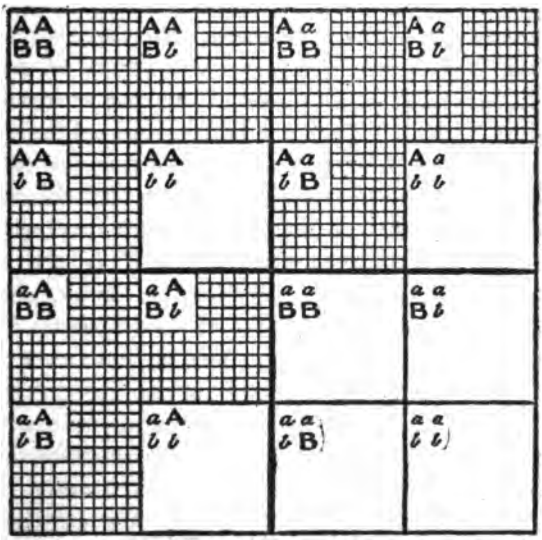
ness (b). The constitution of the F_2 family may be gathered from the accompanying diagram, which is constructed upon the same principle as on p. 40. The interaction of characters lies in the inability of colour, whether grey or black, to appear unless the pigmentation factor (A) is present. All individuals homozygous for (a) must be albino. Albinos carrying the grey factor (B) are constitutionally different from those in which that factor is absent. In appearance, however, the two classes are indistinguishable, and, moreover, any albinos bred together produce albinos alone. But as soon as the pigmentation factor is introduced by a suitable cross, the difference between the two classes of albinos is at once manifest. When crossed with a black, the albino homozygous for greyness ($aaBB$) gives only greys in F_1; that which is heterozygous ($aaBb$) gives equal numbers of greys and blacks, whilst the albino which is homozygous for blackness ($aabb$) gives nothing but blacks. The introduction of the pigmentation factor with the black parent brings about the development of the colour-factor which was all along resident in the albino, but prevented from becoming visible, owing to the masking effect produced by the absence of pigmentation. The ordinary 9:3:3:1 ratio is converted into a 9:3:4 ratio, from the impossibility of separating the last two terms on external appearance. Appropriate

breeding-tests reveal the fact that segregation of the grey and black factors goes on as usual beneath the mask of albinism.

SWEET PEAS.

An even more striking instance illustrating the interaction of factors is that of the sweet pea. All the white sweet peas at present known breed true to whiteness, yet in certain cases, when two whites are crossed, the hybrids are not white, but purple. Again, in other cases the hybrids may be Painted Ladies. The purple is in appearance identical with the form which is still found wild in Sicily, and the Painted Lady is also recorded by some old writers as a wild variety, though it is not known to occur as such at the present day. Both cases may be described as examples of reversion, and for the sake of simplicity we may confine ourselves to the case of the red. The explanation is clear. We are dealing with a case of dihybridism, in which each parent is homozygous for the presence of one of the two factors, and for the absence of the other. Colour is produced only when *both* factors are present in the zygote. Since each white parent brings in one factor, the hybrid must contain both, and must therefore be coloured. In the present case it will be red. If we represent the presence of one factor by *A*, and the presence of the other factor by *B*, *a* and *b* denoting their

respective absence, we may make use of the scheme previously given (p. 40) for a case of simple dihybridism. Of the 16 squares in such a scheme there are 9 in which both *A* and *B* are present, and 7 in which either one or both of these is absent. Consequently, in the F_2 generation we should obtain 9 reds and 7 whites out of every 16 plants. And this is what experiment has



shewn to be actually the case. The 9:7 ratio is in reality a 9:3:3:1 ratio, in which, owing to interaction of the factors, we cannot dis-

generation. Novelties are what the horticulturist wants, and here the new science of heredity has much to teach the practical man. Let us suppose that he has two varieties, each possessing a desirable character, and that he wishes to combine these characters in a third form. He must not be disappointed if he makes his cross, and finds that none of the hybrids approach the ideal which he has set before himself; for if he raises a further generation he will obtain the thing which he desires. He may, for example, possess tall green-seeded and dwarf yellow-seeded peas, and may wish to raise a strain of green dwarfs. He makes his cross—and nothing but tall yellows result. At first sight he would appear to be further than ever from his end, for the hybrids differ more from the plant at which he is aiming than did either of the original parents. Nevertheless, if he sow the seeds of these hybrids he may look forward with confidence to the appearance of the dwarf green. And owing to the recessive nature of both greenness and dwarfness, he can be certain that for further generations the dwarf greens thus produced will come true to type. The green dwarfs are all fixed as soon as they appear, and will throw neither talls nor yellows. The less the hybrid resembles the form at which the breeder aims, the more likely is that form to breed true when it appears in the next generation.

But as all practical breeders know, the fixation of the required type is not always effected as simply as in the case of the green dwarf. Let us suppose that the parents are the same as before, and that the new form now required is a tall yellow-seeded pea. As we have already seen, the hybrids are all of the type required, viz., tall yellows. But they do not breed true. Still, the majority of their offspring (*i. e.*, nine-sixteenths), are tall yellows, and by saving the seed of these and growing further generations, using selection each time, the breeder expects eventually to fix the type. It is at this point that he frequently provides for himself a great deal of unnecessary labour, which a knowledge of Mendelian inheritance would spare him. These tall yellows all look alike to the eye; what, therefore, more natural than to treat them alike, and to jumble up together the seeds collected from the different individual plants. Nevertheless, to do so is to court failure, or at best a tedious success. Out of every nine yellows, one, and one alone, is already fixed, whilst the remaining eight are, by their very nature, bound to throw other forms.* If the

* How this comes about may be easily gathered by referring to the scheme on p. 40. Of the 9 zygotes containing both *A* and *B* (*i. e.*, the factors for tallness and yellowness), 4 are of the constitution *AaBb*, and will therefore give tall yellows, tall greens, dwarf yellows, and dwarf greens in the proportion 9 : 3 : 3 : 1;

breeder saves the seed *from each plant separately,* he will obtain what he wants, and will obtain it ready fixed. The idea that many generations are required for the fixation of a new variety is a wrong idea, and only arose because it was not unnaturally assumed that either plants or animals of identical appearance were also identical in their breeding qualities. To-day we realise that this is not necessarily the case, and Mendel's discovery has introduced principles which must largely modify the breeder's methods. For the points to be borne in mind are two. In the first place, all the possible forms which can emanate from a cross between two fixed strains appear in the sec-

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two are of the constitution *AABb*, and will give tall yellows and tall greens in the proportion 3 : 1; two are of the constitution *AaBB*, and will give tall yellows and dwarf yellows in the proportion 3 : 1; one alone is of the constitution *AABB*, and this will consequently breed true to both the tall and the yellow characters.

As an example of the practical working of these principles, we may briefly allude to the results obtained by Mr. Biffen, of the Agricultural Department of Cambridge University. Working on Mendelian lines Mr. Biffen has been able in a very few generations to build up and fix wheats combining the desirable characters of several varieties. Length of straw, cropping power, 'strength' of grain, immunity to rust—all these he has demonstrated to be unit-characters exhibiting Mendelian inheritance. Using this knowledge he has been able to produce pure strains of wheat which must greatly influence the agricultural outlook in this country when they come to be placed upon the market.

ond generation, provided that a sufficient number are grown; and in the second place, a certain proportion of each of these forms is already fixed in the second generation. Two generations suffice to produce and fix the new variety, and one further generation is all that is required to indicate the fixed individuals.

CROSSING FOR VIGOUR.

Again, since all the possible re-combinations of the characters involved in any cross come fixed in a definite proportion of the individuals of the second generation, it is obvious that the two original parental types will be among them. Now it is a well-known fact that in most cases a cross means increased vigour for the progeny. But the breeder is often shy of making such crosses, for fear of breaking up and losing the desirable combination of characters found in his original strains. Mendel's discovery may reassure him on this head. In three generations he can now reproduce the parental types, and reproduce them with all the increased vigour resulting from a cross.

PURITY OF BREED.

Considerations such as these naturally lead us to ask, What is meant by the term 'pure-bred'? What is the criterion by which we are to judge the pure-bred thing? Until recently we should have

said that this criterion was provided by the pedigree of the individual—that the individual was either more or less pure-bred for any given character, in so far as it could shew a longer or shorter line of ancestors possessing that character. To-day our criterion is an entirely different one. A plant or an animal is pure-bred for any given character when it has been produced by the union of two gametes each carrying that character. The single comb which arises from the union of walnuts, themselves the result of mating rose with pea, breeds as true as does the single of unblemished single ancestry. From a cross between a black and a white rabbit there come greys in the second generation, which breed as true to type as the wild rabbit of irreproachable pedigree. Pedigree is valuable as affording an indication of purity, but the pure-bred thing may, and often does, arise from a stock which is anything but pure. One thing may be pure-bred because of its ancestry, and in spite of its ancestry another may be equally pure. For the one and only arbiter of purity is the gamete.

COUPLING OF CHARACTERS.

Before dismissing the subject of dihybridism a brief allusion may be made to another phenomanon, from which important developments may be expected in the future. In the dihybrid cases

hitherto considered, the two pairs of characters behave quite independently, in so far as the process of segregation was concerned. But in certain cases there occurs a form of coupling between the members of the different pairs. In the sweet pea, purple is dominant to red, and the erect standard is dominant to the 'hooded' standard. The sweet pea, which is heterozygous for both of these pairs, is in appearance an erect purple, and if the case were one of simple dihybridism we should expect its offspring to consist of 9 erect purples, 3 hooded purples, 3 erect reds, and 1 hooded red. Actually, it consists of 2 erect purples, 1 hooded purple, and 1 erect red. And further experiment has shewn that, whilst the hooded purple and the erect red breed true, the erect purples always give both hoods and reds. In the F_2 generation the purples are to the reds, and the erects are to the hoods, as 3:1, but the hood is completely coupled with the purple, and in these strains is never found associated with the red.

In other cases it may happen that the coupling is not complete. Two forms of pollen grains occur in the sweet pea, viz., elongated and round, the former being dominant to the latter. In families where long and round pollen, as well as purple and red flowers, are found, the dominant is to the recessive as 3:1 for either pair. But instead of the purple longs being three times as numerous

as the purple rounds, there is actually but one purple round to about 12 purple longs. The deficiency of rounds among the purples is compensated for among the reds, where the rounds are to the longs in the ratio of about 3.3:1. There is coupling of longness with purple, and of roundness with red, but the coupling is not complete. Few cases of gametic coupling have been as yet worked out, and many points with regard to it are still obscure. Nevertheless, the phenomenon is of great scientific interest, and there is every probability that, as it becomes better known, it will be found of peculiar importance in the elucidation of the architecture of the gamete.

MENDEL AND CURRENT BIOLOGICAL CONCEPTIONS.

Such then are the facts elicited by Mendel and others, and such is the interpretation put upon them. Does all this, it may be asked, affect our conceptions of the nature and origin of living forms? The answer must be in the affirmative. Of the fact of evolution we are certain. Of the workings of natural selection we have no doubt. But with regard to the nature of the variations upon which selection works there is much diversity of opinion. The discoveries associated with Mendel's name have introduced no fresh view here. Nevertheless, they must greatly influence our conception of the part played by the different forms of variation in the evolutionary process. To see

why this is so will necessitate a brief historical digression. More than half-a-century ago Darwin recognised that the problem of the origin of species is inseparably bound up with the nature of variation. The evolution of fresh species depends upon the action of natural selection on the variations that occur in living forms.

VARIATION AND NATURAL SELECTION.

Individuals of a species, which from their variations are more adapted to their environment, survive in the struggle for existence; individuals less adapted are placed at a disadvantage, and tend to perish in the competition with their more favoured kin. The survivors leave offspring, of which some shew the favoured variation in a rather greater, some in a rather less, degree. Natural selection sifts out the former as the parents of the next generation. And so for generation after generation. The process is a cumulative one. By the action of natural selection small variations are gradually worked up into a specific difference and finally fixed. Natural selection is, as it were, the guiding hand that is continually exerting a steady pressure upon the species, and the species, from its inherent variability, is a plastic thing, ever responding to the touch of natural selection. It is true that Darwin recognised that large variations may suddenly arise complete from the first,

and he instances, among others, the cases of the large-crested Polish fowls, and of the familiar short-legged Ancon ram. But he was disinclined to attach much importance to such variations in the production of species, holding that from the rarity of their occurrence they would rapidly become swamped by intercrossing with the normal form. He considered that it was by the action of natural selection on small continuous variations that species had been and were being built up. This idea, supported by the wealth of facts marshalled together by Darwin, dominated thought for forty years. Here and there a dissentient voice was heard, but it was not until ten years ago that Bateson drew attention to the frequency of Discontinuity in variation, and suggested that such saltatory variations may have played an important part in the production of species.

MUTATIONS.

More recently the Dutch botanist, Hugo de Vries, has emphasised this point of view. He considers that the term 'variation' has been used to include several distinct phenomena. There are variations which arise suddenly, and are discontinuous. These de Vries calls **mutations**. They are sharply divided from the stock whence they took their origin, and their inheritance is discontinuous. The mutation may be dominant to

the original form, as for example the rose comb in fowls, which doubtless arose from the single. Or the mutation may be the recessive form, as in the Cupid variety of the sweet pea. The magnitude of the mutation may be great and striking, or it may be comparatively small. But whatever its size, its inheritance would seem to be according to the law of gametic segregation.

EVER-SPORTING VARIETIES.

Another form of variability recognised by de Vries is found among the instances which he terms ever-sporting varieties.* The common snapdragon, *Antirrhinum majus*, is a case in point. There exists a variety of this flower in which the yellow ground colour is relieved by red stripes. This striped variety apparently cannot be fixed. Among the plants raised from its seed there occurs a certain proportion, generally small, which produces red flowers. By selection it is possible to get a strain of snapdragons whose seed gives rise to over 90 per cent. of striped. Similarly, by selection of the red-flowered plants, a strain may be produced which gives about 80 per cent. of red, the rest being striped. In neither case did de Vries succeed in getting a pure strain, either of striped or of red. These ever-sporting

* A free translation of the original terms 'Halb-rassen' and 'Mittel-rassen.'

varieties are undoubtedly complex in their nature, but as far as one can judge from his account, de Vries' experiments do not preclude the possibility of the existence of pure strains of striped and unstriped forms. It seems not impossible that when attention is more closely concentrated on the progeny of individual plants, a strain of reds may be produced which throws no striped, and possibly also a strain of striped which throws no reds. Segregation implies gametic purity, and before we can deny the presence of this phenomenon in the flower-colour of the snapdragon, further experimental work is necessary.

FLUCTUATING VARIATIONS.

Lastly, we must recognise with de Vries the type of variation which he has termed 'fluctuating.' The occurrence of such fluctuations is universal. To say that no two individuals of a species are exactly alike is to reiterate a truism. The tall pea is a distinct race, and the dwarf pea is another. It is probable that the dwarf pea arose suddenly as a mutation from the tall. Having once arisen, it breeds true to the dwarf character. It is the property of a mutation to do so. But the dwarfs are not all of precisely the same height. Some are rather taller, and some rather shorter, than the normal. The dwarf mutation is subject to fluctuating variations which are probably due to the

environment peculiar to each individual. A little more manure in its particular patch of soil, fewer surrounding weeds, greater freedom from the attacks of pests—these, and many other factors, may have contributed to the increased height of a plant as compared with its neighbours. But the fluctuating variations due to these causes are, so far as we know, not inherited. No horticulturist of experience would propose to produce from the dwarf pea a permanently taller race by a process of manuring. There is little doubt, but that the seeds from the richly manured, and those from the normally grown, plant would, when raised under similar conditions, each produce a row of plants indistinguishable in point of size. Nevertheless, the view is generally accepted, that careful selection of fluctuating variations will eventually lead to the improvement of a stock. At first sight this might appear to contradict what has been written above. Probably the truth is, that under the head of fluctuating variations we are dealing with distinct phenomena. Doubtless some of the so-called fluctuations are in reality small mutations, whilst others are due to environmental influence. The difficulty of distinguishing between the two is very great. The simultaneous existence of small mutations and large fluctuations leads to the disguising of the former by the latter. Only careful and laborious analysis will avail us here,

and such analysis is precisely what is at present lacking. The position is roughly as follows. Of the inheritance of mutations there is no doubt. Of the transmission of fluctuations there is no very strong evidence. It is therefore reasonable to regard the mutation as the main, if not the only, basis of evolution. And the great service which Mendel has rendered to this branch of philosophy is the demonstration of the fact, that the mutation, when once it has arisen, is not likely to be swamped by in-breeding with the normal form, provided that it is not injurious to the species. We now recognise discontinuity in inheritance as well as in variation. The new character which arises as a mutation has its representative in the gamete. Once it has arisen, selection alone can eliminate it. Mendel's discovery, then, has led us to alter materially our ideas of the evolutionary process. The small fluctuating variations are not the material on which selection works. Such fluctuations are often due to conditions of the environment, to nutrition, correlation of organs, and the like. There is no indisputable evidence that they can be worked up and fixed as a specific character. Tall peas fluctuate considerably in height, but no gradual process of selecting the shortest will ever result in a permanent race of dwarfs. It is conceivable that the soil may be so doctored as to retard their growth, so that they come to mimic,

as it were, the dwarfs. But remove the special conditions and their true nature will be manifest. A cursory examination of horticultural literature must convince anyone, that it is by selection of mutations, often very small, that the gardener improves his varieties. Evolution takes place through the action of selection on these mutations. Where there are no mutations there can be no evolution. How and why these mutations arise is the great outstanding problem of biology. It is enough here to emphasise their existence, and to see how the recognition of them must modify current ideas.

THE CONCEPTION OF THE INDIVIDUAL.

Our conception of the individual begins to take definite shape, and in place of the vague indefinable something by which we were content to mark off one individual from another, we have now a definite criterion in the unit-character. The individual is an aggregate of unit-characters, and individuality is the expression of a particular aggregation of such characters. Though often reacting upon one another, the factors on which these characters are based behave as independent entities during the hereditary process, and heredity in consequence we may regard as a method of analysis, enabling us to judge of the number and condition of the unit-characters which go to make up the individual. The facts of heredity provide us with a

series of reactions, which, if read aright, reveal to us the constitution of the living thing. And in the constitution of the living thing we have the key to its behaviour, to its potentialities and limitations, to what it can become, and what it can produce.

The position of the biologist of to-day is much the same as that of the chemist a century ago, when Dalton enunciated the law of constant proportions. In either case the keynote has been Discontinuity—discontinuity of the atom, and the discontinuity of the variations in living forms. With a clear perception of this principle, and after a long and laborious period of analysis, the imposing superstructure of modern chemistry has been raised upon the foundation of the atom. Not otherwise may it be with biology; though here, perforce, the analytical process must be lengthier, both from the more complex nature of the material, and from the greater time involved in experiments on living forms. For unlike the chemist, the biologist is trammelled by the times and seasons. Nevertheless, the achievements of the last few years are such as to warrant us in looking forward hopefully to the time when our progress in the knowledge of the living may bear comparison, not unworthily, with the science of the things that are without life.

ECONOMIC ASPECTS OF THE DISCOVERY.

Meanwhile, a few words on the general aspects of the conceptions that have arisen from Mendel's discovery may not be out of place in this connection. Economically their influence must be very great. Since the principles of heredity form the very basis of the breeder's operations, anything which throws new light on these hitherto obscure matters must largely influence an important industry. From the little that has already been found out, the breeder is enabled to proceed with some degree of certainty. Till now his methods have been almost entirely empirical, and in great measure wasteful. He has bred together those that seemed likely to produce what he required. From their numerous offspring he has selected those few that seemed to come nearest to what he wanted. The rest, and these the great majority, must be rejected. Many be called, but few chosen. True, the end aimed at, fixation, is eventually attained. But its accomplishment entails much unnecessary waste by the way. Mendel's discovery must react strongly upon these methods. As soon as he recognises the definiteness of his problems; as soon as he realises the conception of unit-characters and their mode of inheritance—the breeder will reach his end more swiftly and more surely, with greater economy of time and of material. Few individ-

uals, comparatively, will suffice for his preliminary process of analysis, and when this has been done, he may pass to greater numbers with a feeling of certainty as to the result. He will now know with what he is dealing. The possession of a transmissible character, desirable or otherwise, is no longer a question merely of degree. Either the individual has it, or has it not. Either it is represented in his gametes, or it is not. Once its presence or absence has been determined by analysis, the line can be definitely drawn. The breeder may proceed to build up synthetically, character by character, the plant or animal which he requires. His chief limitations will be those imposed by Nature upon the variations of living forms. These he will learn from simple observation and experiment, thereby saving time and labour in futile attempts to achieve the impossible. For he will have read the riddle of the blue Andalusian fowl.

CONCLUSION.

In conclusion, a few words upon another aspect of Mendel's discovery. How the discovery arose from the accurate analysis of a simple instance we have already seen. How the principle of gametic segregation applies to numerous cases in plants and animals has been pointed out. That it must apply to man also—the most complex of living forms—evidence already exists. If there is aught

in these matters, the time is coming when they must be taken into account by those whose business is with the ruling and advising of their fellow-men; whose wish is to leave the world a little less aimless than they found it; who desire not "promiscuously to swim down the turbid stream and make up the grand confusion." Most of us are agreed that the circmustances of modern life are susceptible of change and of improvement. That end we seek to attain by better teaching and better sanitation. And in this direction we have made a start by concentrating attention upon the lower strata of society. Speaking broadly, our present policy aims at raising the standard of the less fit; at attempting to bring them closer by such means to those who are richer in natural endowment. Has such a line of endeavour any hope of permanent success? Or is it based upon a misconception of the nature of living things? Some there are, doubtless already, who question whether the general policy pursued with regard to the lowest classes of the nation is a sound policy; who are troubled with the suspicion that Hygiene and Education are fleeting palliatives at best, which, in postponing, but augment the difficulties they profess to solve. To them the facts of heredity may speak with no uncertain voice. Education is to man what manure is to the pea. The educated are in themselves the better for it, but their experience

Manure is full of ——, q.e.d. education is full of it also.

so true.

will alter not one jot the irrevocable nature of their offspring. Permanent progress is a question of breeding rather than of pedagogics; a matter of gametes, not of training. As our knowledge of heredity clears, and the mists of superstition are dispelled, there grows upon us with ever-increasing and relentless force the conviction that the creature is not made but born.

NOTE

As some readers may possibly care to repeat Mendel's experiments for themselves, a few words on the methods used in crossing may not be superfluous. The flower of the pea with its standard, wings, and median keel is too familiar to need description. Like most flowers, it is hermaphrodite. Both male and female organs occur on the same flower, and are covered by the keel. The anthers, ten in number, are arranged in a circle round the pistil. As soon as they are ripe they burst and shed their pollen on the style. The pollen tubes then penetrate the stigma, pass down the style, and eventually reach the ovules in the lower part of the pistil. Fertilisation occurs here. Each ovule which is reached by a pollen tube swells up and becomes a seed. At the same time the fused carpels enclosing the ovules enlarge to form the pod. When this, the normal mode of fertilisation, takes place, the flower is said to be selfed.

In crossing, it is necessary to emasculate a flower on the plant chosen to be the female parent. For this purpose a young flower must be taken in which the anthers have not yet burst. The keel is depressed, and the stamens bearing the anthers are removed at their base by a pair of fine forceps. It will probably be found necessary to tear the

keel slightly in order to do this. The pistil is then covered up again with the keel, and the flower is enclosed in a bag of waxed paper until the following day. The stigma is then again exposed and dusted with ripe pollen from a flower of the plant selected as the male parent. This done, the keel is replaced, and the flower again enclosed in its bag to protect it from the possible attentions of insects until it has set seed. The bag may be removed in about a week after fertilisation. It is perhaps hardly necessary to add that strict biological cleanliness must be exercised during the fertilising operations. This is readily attained by sterilising fingers and forceps with a little strong spirit before each operation, thereby ensuring the death of any foreign pollen grains which may be present.

The above method applies also to sweet peas, with these slight modifications. As the anthers ripen relatively sooner in this species, emasculation must be performed at a rather earlier stage. It is generally safe to choose a bud about three parts grown. The interval between emasculation and fertilisation must be rather longer. Two or three days is generally sufficient. Further, the sweet pea is visited by the leaf-cutter bee, *Megachile,* which, unlike the honey bee, is able to depress the keel and gather pollen. If the presence of this insect is suspected, it is desirable to guard against

the risk of admixture of foreign pollen by selecting for pollenating purposes a flower which has not quite opened. If the standard is not erected, it is unlikely to have been visited by *Megachile*. Lastly, it not infrequently happens that the little beetle *Meligethes* is found inside the keel. Such flowers should be rejected for crossing purposes.

APPLIED HEREDITY

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FEW subjects touch man so closely as heredity, yet upon few is widespread ignorance more prevalent. The extreme complexity of the problems involved and the absence of any clear guide to the method of attacking them have discouraged scientific men from devoting their energies to these studies. Yet the knowledge to picture clearly the workings of heredity, to predict the outcome of this or that given mating, would give to man such powers of control over the living world as only a romancer has ventured to dream of. It is not generally known that the beginnings of that knowledge already exist, and that the great and baffling problem of heredity has suddenly passed from the speculative to the experimental stage. The credit of it belongs to one man. More than forty years ago Gregor Mendel, an Austrian monk, showed clearly that heredity was no mystery, but a natural phenomenon open to attack by the scientific method of observation and experiment.

The son of Silesian peasants, Mendel was destined for the Church, and early entered the Augustinian monastery of Brünn. But he had the

opportunity of studying natural science for a few years at Vienna, and became much interested in the problems of heredity. With the intuition of genius he saw wherein others had failed, and in his cloister garden he carried out with peas that series of experiments which have since become so famous in the scientific world. His results were 42 years old published in 1865, in a brief paper of less than fifty pages—a paper that for clearness of exposition and magnitude of issue can be compared only with William Harvey's classic treatise on the circulation of the blood.

Yet no man heeded it, for all were intent on other things. Mendel's paper remained forgotten, buried in the proceedings of a local natural history society. Only with the dawn of the present century was it unearthed, and men of science began to realize the greatness of the achievement. Since then Mendel's results have been confirmed over and over again. The principles which he enunciated have been shown to hold good alike for animals as well as plants. Upon the foundations which he laid men have begun steadily to build up that accurate knowledge of heredity which in course of time will modify profoundly our attitude towards living things.

In what does the revolutionary nature of these doctrines consist? Let us take a simple case. Rose-comb bantams are of two kinds, blacks and

whites, and pure strains of either kind breed true. Now cross the black with the white. Instead of being of an intermediate color, the offspring are all black like the black parent. For this reason black is said to be dominant to white, which is spoken of as recessive. When the hybrid blacks are bred together they produce blacks and whites in the proportion of three of the former to one of the latter. The whites so formed thenceforward breed true, and throw no blacks, in spite of their black ancestry. The blacks, however, are of two kinds—(1) pure dominants, which give only blacks when mated with a white bird, and (2) impure dominants, which behave like the original hybrids when mated together, giving blacks and whites in the ratio three to one. Moreover, such birds when crossed with whites may be shown experimentally to produce equal numbers of blacks and whites.

For a group of facts such as this Mendel provided a simple explanation. The formation of a new individual, as is well known, is the result of the union of two germ-cells, of which one is provided by each parent, the spermatozoon or pollen grain by the male, and the ovum or egg-cell by the female. In the case of the rose-comb bantams we are dealing with the inheritance of two alternative characters, blackness and whiteness. The central idea of the Mendelian theory is that any given germ-cell can contain only one of these alternative

characters. Such characters, which are transmitted as separate units, are known as unit-characters. In the present instance every germ-cell must carry either blackness *or* whiteness, but it cannot carry both. When a "black" germ meets another "black" germ the result is a pure dominant black chicken, which itself can produce only black

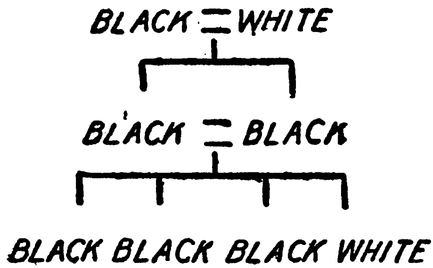


DIAGRAM I, ILLUSTRATING THE DOMINANCE OF BLACK TO WHITE IN ROSE-COMB BANTAMS

germs. When a "white" germ meets a "white" germ a white chicken results which can give rise to "white" germs only. And when a "black" germ meets a "white" germ the resulting bird is in appearance a black, because blackness is dominant over whiteness. But when such a bird comes to form germ-cells the black and the white characters separate from one another and pass singly into the germ-cells. Hence a bird which has been formed by the union of a "black" and a "white" germ-cell does not form "gray" germ-cells, but forms

equal numbers of "black" and of "white" germ-cells. The breeding together of the hybrids therefore implies the coming together of two sets of germ-cells, each consisting of equal numbers of blacks and whites. As is graphically shown in diagram 2, this can lead to one result only, viz., the production of a number of offspring, of which one quarter are formed of the union of two "black" germ-cells, one quarter by union of two "white" germ-cells, and two quarters by the union of a black and a white. These last, like the original hybrids, will be black to the eye, because blackness is dominant to whiteness where both exist in the same individual. Consequently the result of breeding together the hybrids is the production of blacks and whites in the ratio three to one.

Let us now see what happens when the members of such a family are bred on for a further generation. In the first place the whites bred together breed true, and this in spite of the fact that their parents and most of their brothers and sisters are black. They can never give blacks, because the black character has been split clean out of the germ-cells from which they arose. Of the blacks there are two classes, of which one is twice as numerous as the other. These are the hybrid blacks formed by the union of a "white" and a "black" germ-cell, and when bred together they behave like the original hybrids in that a quarter

of their offspring are whites. The other class of blacks consists of those formed by the union of two black germ-cells. These breed as true to blackness as the original pure black grandparent. It is here that the great practical importance of Mendel's discovery lies. When a cross is made between two pure strains which differ from one another in respect of a single pair of characters only, the second generation will contain a definite proportion of individuals which breed as true to the characters they exhibit as did the original parents. The white rose-combs of the second generation, in spite of their black ancestry, are as pure and uncontaminated by blackness as the original white parental strain.

Such is Mendelian inheritance in its simplest form. Recent experimental work has shown that it is a phenomenon of wide if not of universal occurrence among living things. During the past few years it has been demonstrated for such varied characters as structure, size, shape, color, and fertility among plants, as well as for numerous characters in animals. To mention but a few examples: tallness is dominant to dwarfness in peas, sweet peas, and snapdragons; color is dominant to white, and purple is dominant to red, in stocks and sweet peas; palm leaf is dominant to fern leaf in Primulas, and in the same genus double flowers are recessive to single; in Hyoscyamus the biennial

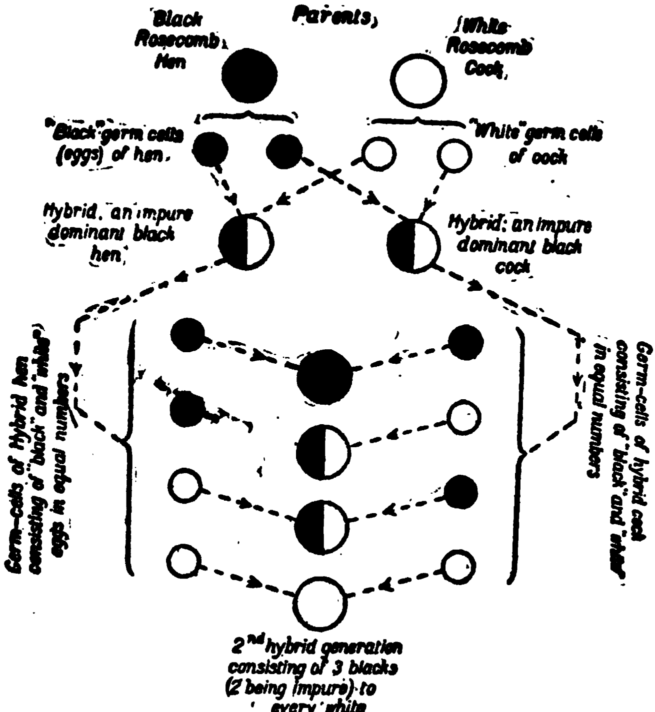


DIAGRAM II, ILLUSTRATING THE INHERITANCE OF THE BLACK AND WHITE CHARACTERS IN ROSE-COMB BANTAMS

flowering habit is dominant to the annual; in the sweet pea sterility of the pollen is recessive to the normal fertile state. Among animals, the long An-

gora hair is recessive to short hair in rabbits; color is dominant to albinism in rabbits, rats and mice; chestnut is recessive to bay or brown in horses; the peculiar waltzing habit of the Japanese mouse is recessive to the normal condition; while in fowls, which have been much used for these experiments, numerous Mendelian characters have been demonstrated for the structure and color of the plumage, the form of the comb, the color of the skin, and many other features.

So far we have only dealt with cases in which the individuals crossed differ in but a single pair of characters. It more frequently happens that the original parents differ in many characters, and such a cross may often appear to result in a hopeless tangle. Nevertheless, in many cases careful scrutiny will reveal an underlying simplicity of arrangement. Each pair of characters in which the original parents differed is transmitted according to the simple Mendelian rule, and is usually transmitted independently of any other pair. For example, color is dominant to white in the flowers of the pea. And the tall habit of the ordinary garden pea is dominant to the dwarf habit of peas like American Wonder, which average about eighteen inches only. Here, then, we have two pairs of differentiating characters. Let us suppose that one of the plants to be crossed is a tall with white flowers, and the other a dwarf with colored flowers.

The resulting hybrids must be tall, and must also have colored flowers. For tallness is dominant to dwarfness, and color is dominant to white.

The offspring of such hybrids will, according to the Mendelian rule, consist of three talls to each dwarf; and at the same time there will be three plants with colored flowers to every plant with white ones. Therefore, this generation consists of four classes of plants, viz., tall colored, tall white, dwarf colored, and dwarf white, in the ratio of 9 : 3 : 3 : 1. A combination of characters has been brought about, and two new classes of peas, colored talls and white dwarfs, have been formed. Moreover, as theory demands and experience confirms, a certain definite proportion of each of the four classes is fixed in this generation. By picking out such plants the two new varieties may be established in the short period of three generations. The great economic importance of these results may fitly be illustrated by a short account of some experiments on wheat now being carried on by the Agricultural Department of Cambridge University.

So long ago as 1890 the National Association of British and Irish Millers called attention to the fact that the quality of English wheats had deteriorated. For milling purposes the foreign article with its strong glutenous grains was found to be greatly superior, and English wheats were selling at 28s. 6d. a quarter, while Manitoba hard was

fetching 35s. The National Association endeavored to interest the agricultural societies in the question, but found that they were more or less resigned to this unsatisfactory state of things, and despaired of competing with the superior quality of the foreign wheat. Indeed, many declared that grain of the highest quality could not be grown profitably in Great Britain. At this point the Association took a wise and, for England, a courageous step. They decided to provide the funds for experimental research, and in 1900 Professor Biffen of the Cambridge University Agricultural Department started his remarkable series of experiments. It was just at the time of the rediscovery of Mendel's paper. Thanks to Professor Bateson, the extreme importance of that paper was at once recognized in Cambridge, and Professor Biffen organized his work upon Mendelian lines. He collected together all the varieties he could lay hands on, and by numerous crossing tests he laid the foundations of an accurate knowledge of the various unit characters that occur in wheat. He found the beardless character to be dominant to beardlessness, rough chaff dominant to smooth, red grain to white grain, thick stem to thin stem, and so on. Early and late ripening behaved as a Mendelian pair of characters, as also did heavy as opposed to poor cropping capacity. Professor Biffen's analysis further revealed Mendelian heredity in two char-

acters of such importance as to deserve especial mention. We have already seen that the poor quality of English wheat is due to poverty of glutenous matter. The grain is too starchy, and requires the admixture of a considerable amount of glutenous "strong" foreign wheat to give flour which will bake into a presentable loaf. Professor Biffen has been able to show that the highly glutenous grain is dominant to the starchy one. With this knowledge he has been able in a few years to produce a wheat combining the large cropping capacity of English wheat with the high gluten content of a foreign variety.

But the most important and the most fascinating of all Professor Biffen's experiments concern the inheritance of an entirely different character. In all countries the most serious enemy of the wheat farmer is rust. Early in their growth the plants are attacked by a parasitic fungus whose presence is rendered conspicuous by an abundant outbreak of reddish-yellow pustules all over the foliage. In certain seasons and with certain varieties the outbreak may be so severe as to very greatly diminish the yield of grain. In the bad rust year of 1891 the loss due to this cause in Prussia alone was calculated at over £20,000,000, while a well-known authority estimates that the average loss from rust to the wheat crops of the world would not be covered by £100,000,000. No prophylactic against

the disease has been discovered, and it is recognized that the only way to avoid it is to make use of varieties which are naturally immune. Unfortunately the few such varieties that exist are in other respects poor and unprofitable to grow.

Professor Biffen began his experiments by crossing a variety peculiarly subject to the attacks of yellow rust with an immune variety. The hybrids produced were all severely attacked by rust. In the following year such seed as could be collected from these plants was sown. The greater number of the resulting plants were much rusted, but some were entirely free from the disease, though growing up in the closest contact with their rusty brethren. It was found on counting that the immune plants formed almost exactly a quarter of the total number. In other words, the experiment proved susceptibility and immunity to be a pair of Mendelian characters, and consequently within the control of the breeder to combine with other characters according as he pleased. The fact that resistance to yellow rust is a unit character exhibiting Mendelian inheritance makes it a simple matter to transfer it to wheats which are in every way desirable except for their susceptibility to rust. From the knowledge gained through his experiments Professor Biffen has been able to build up wheats combining the large yield and excellent straw of the best English varieties with the

strength of the foreign grain, and at the same time quite immune to yellow rust. During the present year several acres of such wheat coming true to type were grown on the Cambridge University Experimental Farm, and when the quantity is sufficient to be put upon the market there is no reason to doubt its exerting a considerable influence on the agricultural outlook.

Besides the work on wheat, experiments have been undertaken with barley. As with the wheats, there are varieties of barleys with glutenous and others with highly starchy grains. The more starch a barley contains, the more valuable it is for malting purposes. Since Professor Biffen has been able to demonstrate that with barley, as with wheat, starchiness is recessive to glutenous quality, it should be an easy matter in the future to associate the starchy character with other valuable properties in barleys.

Nor is the work at Cambridge confined to plants. A start has been made with the object of investigating the inheritance of horns and of face color in sheep, and Professor Wood has been able to show that both these characters are inherited upon Mendelian lines. In this way he has been able to combine the hornless character of the black-faced Suffolk with the white face of the horned Dorset. Similarly, Professor Spillman has adduced evidence to show that the polled character in cattle is

dominant to the horned state, thus making it possible to dehorn painlessly any breed of cattle where this is thought desirable.

In all experiments conducted on these lines the method is the same. The breeder sets to work on his living material just as the chemist in the laboratory investigates the properties of an unfamiliar substance. He starts by analysis. Appropriate crossing best enables him step by step to determine the unit characters which go to make up the plant or animal upon which he is working. Once these characters are determined, a knowledge of the Mendelian principles will enable him to combine them together according to his will, and to build up and fix a plant or animal having the properties which he considers most to be desired. No long and tedious method of selection is necessary. The new variety may be built up and fixed in three or four years. But the preliminary process of analysis is indispensable, and it is here that the chief difficulties of the work lie. The analysis of a complex chemical substance is often a lengthy and tiresome business. But it is simplicity itself in comparison with the analysis of the properties of the living thing. There is no plant or animal of which the analysis yet makes any pretence to completeness. As the breeder pursues his investigations he is constantly confronted with the unexpected. It is improbable that he will go far with-

out encountering the curious and, until recently, mysterious phenomenon of reversion on crossing. White sweet peas breed true to whiteness, but it sometimes happens that the plants produced when two whites are crossed are not only fully colored, but their color is that of the wild purple Sicilian form. Color here is, as it were, a compound character. Two things are necessary for its production and unless both are present the flower will be white. Each of the white parents in our cross contained one of the two things necessary for the production of color, and each of the two things is transmitted independently, according to the Mendelian rule. Crossing brings these two things together, and straightway the color appears.

The case of the sweet pea may be paralleled among fowls, where a cross between certain strains of true-breeding whites results in the production of fully colored birds approximating to the ancestral black-red.

Again, the cross between a black and an albino rabbit results in certain cases in the production of animals with the gray-brown coat of the wild form.

Many cases of similar nature have now been investigated, and to-day we realize that these peculiar instances of reversion, so mysterious to the older naturalists, are part of the orderly process of heredity, and equally amenable to control with the simpler cases mentioned above.

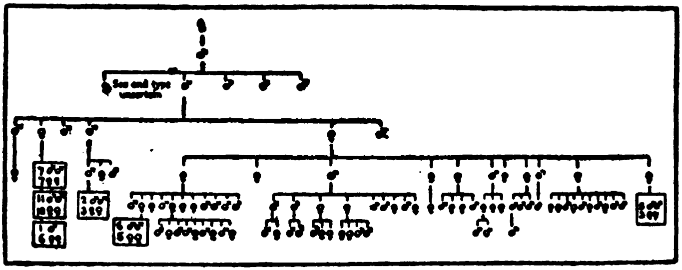
There are other phenomena in heredity which at present are less understood. Characters may be associated together in a peculiar way. In the sweet pea the hooded character is recessive to the old-fashioned erect standard, and red is recessive to purple. But in certain families where both reds and purples as well as flat and hooded standards occur, the hooded character is never found dissociated from the purple. All the reds have the erect standard. Yet the hooded red is not a physical impossibility, for it is well known to exist in other strains. The subject is at present obscure, and much experimental work will have to be done before it is cleared up. Not until then shall we be able to realize its bearing upon economic problems.

By this time the very great importance of Mendel's discovery will doubtless be apparent. Through it heredity emerged from the mysterious and the nebulous and took its place among the exact sciences. Yet no one realizes more than those who are actively attacking its problems how little has been achieved, how vast are the fields still to be conquered. But each new problem unravelled puts a fresh tool into man's hands and helps him towards that control over the organic world without which he cannot make full use of the living resources of the earth. It matters little with what material the experimenter works, whether mice or cereals, primroses or poultry. He will make use

of that which can be most readily supported by the means at his disposal and promises the speediest answer to his questions. For it may well be that a problem solved in rats or butterflies will clarify obscure phenomena in the breeding of cattle or potatoes; and it is upon these seemingly irrelevant experiments that much of the future progress in agriculture will depend.

But how about ourselves? What of man? These are questions which the reader has doubtless asked already. Though little is yet known, the answer need not be ambiguous. Man, too, is subject to those same laws of heredity that govern the transmission of characters in plants and in other animals. Man is among the most complex and slowly breeding of living things, and the investigator is further handicapped by having to rely for his data upon the haphazard and inextricable experiments which are the outcome of civilized marriage customs. Nevertheless a few clear cases have already been worked out, nor are indications wanting that the next few years will witness a considerable extension of our knowledge. One of the most beautiful cases is that of the transmission of a peculiar condition known as brachydactyly. In people affected with this malformation the joints of the fingers and toes are two instead of three, and the whole body is markedly stunted. Dr. Farabee in America and Dr. Drinkwater in England have

demonstrated clearly that this condition behaves as a simple dominant to the normal state. The chances of two brachydactylous individuals marrying are very small, and such people are practi-



PEDIGREE OF A BRACHYDACTYLOUS FAMILY.

♀ ♂ Denote normal males and normal females respectively. Similarly, ♀ ♂ represent brachydactylous males and females. Every individual represented as having issue was married to a normal. It will be noticed (a) that an affected individual always has one affected parent; (b) that about one-half of the children of an affected parent are affected while the rest are normal; (c) that the children normals when married to normals are never affected, in spite of the family history.

cally always the offspring of a brachydactylous and a normal person. They are impure dominants, and they necessarily transmit the peculiarity to one-half of their children on the average. It is an equal chance whether the child of such a union is affected or normal. But when the recessive normal appears it breeds true to the normal state, no matter what the family history for brachydactyly may have been (*cf.* diagram).

Another interesting human case is that of eye-

color. All colored eyes have pigment at the back of the iris. In addition to this there is frequently some yellowish-brown pigment on the front of the iris. The color of such eyes appears as green, hazel, brown, or deep brown, according to the amount of the yellow-brown pigment. Where it is absent the color of the eyes is blue, gray or violet. It has been recently shown by Mr. C. C. Hurst that the condition in which the pigment is present is dominant to that in which it is absent. Blue-eyed children may spring from brown-eyed parents, but the biologist would regard with some surprise the brown-eyed child sprung from parents whose eyes were blue.

The hereditary transmission of disease, to use the word in its widest sense, has for long been a subject of interest to the physician, and men are beginning to inquire how far the Mendelian laws are operative in this sphere. Already there exist clear indications that certain abnormal conditions, such as congenital cataract of the eyes, alcaptonuria, diabetes insipidus, and others, are of the nature of simple Mendelian cases. In others again, such as color blindness and the peculiar disease known as hæmophilia or "bleeding," the inheritance is more complex. The disease is almost confined to the male sex, though transmitted through the unaffected females to their male offspring. Nevertheless, recent experimental breeding among

animals has revealed similar peculiarities of inheritance, and their solution is not unlikely to afford the key to the problems offered by these curious sex-limited diseases. And Professor Biffen's classic experiments with wheat rust have opened up a fascinating field of research in connection with the problems of immunity. If we wish to build up a knowledge of the heredity of human disease, the method at any rate is clear. We must have full and accurate pedigrees, and for their interpretation we require carefully devised experiments in the breeding of plants and animals. With increase in knowledge will come powers of prevention far greater than those we have to-day. How far we may use these powers must rest with the future to decide.

OLD BOTTLES

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London, October, 1908.

IT is probable that the dawn of the twentieth century will long be regarded as a landmark in the progress of scientific thought. Curiously enough, the two branches of natural knowledge affected are the most and the least precise. At the time when radium was setting the physical world in a ferment, biologists began to hear of the discovery in heredity which bears the name of Mendel. But the naturalist has shown less avidity for the new wine than his brother the physicist. Sceptical of precision in a world of flowing variation, he views with suspicion, natural enough, a claim to reduce his knowledge to the exactitude of a science. Hitherto a certain saving vagueness in his articles of faith has modified the discordance between old theory and new fact. And already the reconciler is at work. Professor Thomson is well known as a serious and popular writer on natural history,* and we do not doubt that this work on heredity, heralded in the press for nearly two decades, has been looked forward to with keenness by many who desire to know more of these matters. Let us say at once that the work has its value. The author is evidently in earnest, and has the good of

* *Heredity*, by J. Arthur Thomson. London, 1908.

his species at heart. He has consulted a great many writers, and the numerous quotations scattered through the volume form an interesting record of opinion. Moreover, the bibliography at the end of the book is well arranged, and will doubtless be of service. Nevertheless, it is an unsatisfactory and an unsatisfying book.

Nor is the reason far to seek. It has no plan. Ten years ago no plan was possible. The facts of heredity then formed a confused medley, without central thread or clue by which they could be related to one another. Their classification depended entirely on the idiosyncrasies of the individual mind. It was possible for any one interested in the subject to turn out a creditable book with no more elaborate apparatus than pen, ink, scissors, and a pot of paste. Professor Thomson's book has appeared ten years too late. Ostensibly, of course, it has been brought up to date, and a chapter on Mendel's law has been sandwiched in about halfway through the volume. One cannot help feeling that the author was ill advised in placing it where he has. Had it figured as an appendix, its position would have been more in keeping with the general tenor of the writing, while at the same time it would not have interfered unduly with the symmetry and balance of the remainder of the book. Indeed, we feel that it would have contributed to the artistic unity of the work if the

Mendelian teaching had been altogether ignored. The new wine has had a sad effect upon the old bottles. Perhaps an example may serve to illustrate our meaning. Round the term Reversion, Professor Thomson has written a whole chapter. "Reversion," he tells us, "is the reassertion of latent characters inherited from a more or less remote ancestor" (p. 133). So far, good. Reversion is a time-honoured term and should be respectfully defined. But how remote must a "throw-back" be to constitute a reversion? "It is," writes Professor Thomson, "a normal and frequent fact of inheritance that an offspring should re-exhibit the peculiarity of a grandfather, though neither of the parents showed it. There seems little utility in calling a very frequent occurrence like this a reversion, though it is of the same general nature." We must not cheapen our time-honoured term: what then are we to do? Professor Thomson guardedly suggests that these "minor family throw-backs" should be called "atavisms," and that the word reversion should not be used "unless the throw-back is to an ancestor more than two generations antecedent." Here, then, is a simple criterion between those two different things, an atavism and a reversion. By the introduction of a time element we are able to preserve both our time-honoured terms for future conjuration.

Now let us pour in a few facts. A purple sweet

pea gives a mixed progeny of purples and whites. From these two whites are chosen and crossed together. All the resulting plants are purples. Manifestly this is atavism. Next the two whites are each grown on by means of natural self-fertilisation for a few generations. They produce nothing but whites. At the end of this time they are crossed again. The resulting plants are all purple. Since the throw-back is now "to an ancestor more than two generations antecedent," we must regard this as an instance of reversion. Yet in each case the purples are quite indistinguishable, and when they themselves are bred from they behave in a precisely similar way and give a perfectly straightforward Mendelian result. It takes two things to make a purple sweet pea. If either of these two factors is absent the flowers are white. The two whites in the above experiment each contain one of the two factors. When they are out comes the purple colour. It makes no difference whether the whites have been bred apart for crossed, the two factors are brought together and two or twenty generations. The condition under which the purple appears is the bringing together of those two factors. Experiments such as this have thrown an entirely new light upon reversion, and it is now within the power of the breeder to produce strains of sweet peas, rabbits, or pigeons guaranteed to revert to the wild form, and other

strains, visibly indistinguishable from these, in which reversion will not occur. Had Professor Thomson frankly based his chapter on recent Mendelian experiment he would have been able to present his readers with a shorter and more coherent account of an interesting hereditary phenomenon, and at the same time have spared himself a stupid and rather ridiculous dilemma.

In his preface Professor Thomson expressly states that he has "tried to avoid partisan handling of any theme," and with the volume before us as evidence we can well believe this to be the ideal that he has set before him.

> "'This I have read in a book,' he said, 'and that was told to me,'
>
> "'And this I have thought that another man thought of a Prince in Muscovy.'"

Professor Thomson speaks such diverse messages through so many mouths that the average reader should have little difficulty in arriving at the same indefinite frame of mind as the author. The ideal is such a high one that we are sure he would be the first to welcome any notice of little divagations from the straight and narrow path. And we feel the less compunction in pointing to such slips because we feel certain that our author will not escape his meed of applause from Berkeley Square. In a special section on Non-Mendelian Results (p. 382) Professor Thomson writes as follows—

"Tschermak crossed a white-flowered pea

(*Pisum sativum*) with a red or purple species (*Pisum arvense*); the hybrid progeny resembled the latter; the red colour was dominant. But when these were fertilized from their kind, they yielded, out of 397 plants, 239 red, 75 rose, and 83 white—a proportion of 9 red, 3 rose, and 4 white, which cannot be called Mendelian. . . .

"Tschermak went on to work with the red (239), rose (75) and white (83) plants, fertilising each type from its own kind, and he found that of the reds some produced red and others white and rose-coloured offspring, that of the whites the offspring were mostly white, while most of the rose-coloured plants yielded only a rose-and-white progeny. This, again, does not seem to be a Mendelian result."

He who reads these paragraphs might well be forgiven for failing to realise that he was reading an account of one of the most telling Mendelian experiments yet made. Nevertheless this is actually the case. Any one with an elementary knowledge of the subject knows that the ratio 9:3:4 is one of the most frequent with which the experimenter meets. It has been demonstrated over and over again in animals as well as in plants. We need scarcely add that the subsequent behaviour of Tschermak's plants, which seems to puzzle Professor Thomson so much, is only what the Mendelian interpretation leads us to expect. We do

not consider it necessary to follow Professor Thomson further in his exposition of the Mendelian interpretation of hereditary phenomena.

We fear that we may have conveyed the impression that Professor Thomson *never* makes a statement on his own authority. Happily we are in a position to do the author justice on this head. By careful search through the five hundred odd pages of his book we have discovered certainly three original contributions to knowledge. We trust we shall be pardoned if in the elation of discovery we allow ourselves to dwell a little upon them. The first concerns sheep (p. 366). "When half-bred sheep, resulting from Border Leicester rams and Cheviot ewes, are inbred, they breed *true to their own type*, which is a distinctly non-Mendelian phenomenon." The italics are Professor Thomson's, and must be taken as indicating that he is fully alive to the extraordinary interest of this case, so unlike what usually occurs in the cross-breeding of animal stocks. Curiously enough, in a later page the author tells us that an experienced breeder expressed to him the conviction that the Mendelian formula (which formula?) does not apply in the case of half-bred sheep, instancing the Cheviots and Border Leicesters. But, valuable as such an opinion may be, we cannot suppose that a scientific man would state without reservation a fact of this importance unless he had most accurate

and carefully analyzed data to go upon. By some oversight Professor Thomson has omitted to mention these data, but we trust that he may shortly see his way to laying them before the scientific world.

Professor Thomson's second contribution has to do with man. "The progeny of a white and a black," he writes (p. 384), "is a mulatto, and mulattos intermarrying breed true, neither white nor black reappearing. It is a clear case of blended inheritance, and of blended inheritance remaining stable. And this applies to the hair as well as to colour. . . . There is not the least hint of Mendelian inheritance." We are aware of no body of carefully collected evidence which could justify such a statement, and we can only infer that Professor Thomson has access to some store of information far more complete than any that has yet seen the light. We trust that he will not allow his modesty to continue to hinder its publication. For the possession of such information we could even gladly welcome a second edition of his book.

Of Professor Thomson's third contribution we confess ourselves a little doubtful. But the Heredity of Sex is a subject to which he has devoted so much attention that we feel certain his summing up must possess a peculiar value. "On our view," he writes (p. 497), "the difference between a gamete which produces a male and another which

produces a female is what we can only vaguely call a difference in 'physiological gearing.' . . ." We frankly confess ourselves intellectually incapable of sinking to the profundities whence this utterance emerged. But our anxiety to do justice to Professor Thomson's originality, and the pains at which we have been to extract this little crystal from a superabundant and cloudy mother-liquor, have impelled us to secure it for the admiration of the reader. Nor must we forget to draw attention to the remarkable diagram on page 500. It is true that several pages intervene, but we feel confident that two things of which the meaning is so little obvious must be connected in some such subtle and indefinable way as to dispense with mere accidents of juxtaposition.

It would be unprofitable to devote more space to the consideration of Professor Thomson's book, for we think it unlikely that any one again will undertake a serious work upon heredity without the knowledge which actual contact with the facts can only supply. Indeed, such a work may be compared to a practical treatise on golf written by one who had never handled a club; and if the public took heredity as seriously as golf, it would have about the same value. He who is engaged in experimental research becomes gradually conscious of the development within him of a new faculty—an instinct towards the truth. Through his own

labours he realises with the insight of sympathy the difficulties of others, and the remembrance of his own failures teaches him discrimination in the acceptance of their results. He can tell at once when the metal rings true. For this instinct no amount of cataloguing of other men's opinions will ever provide an adequate substitute. Only the spirit that comes from research can quicken with life the valley of dry bones.

Those who pursue the study of heredity by the method of observation and experiment have of recent years been favoured with not a little distinguished criticism, and the present summer has been rendered remarkable for them by articles from the pens of Dr. Wallace and Professor Poulton. Dr. Wallace's attitude towards these new studies is untroubled by doubt, and his veteran vigour of expression is so refreshing that we offer no excuse for the following somewhat lengthy excerpt:—

> "To any one who has devoted a considerable portion of his life to the study of nature, both in field and in cabinet, both at home and in distant regions, the vast complex of phenomena presented by the organic world, with its endless specific forms, their myriad relations and adaptations, the laws of their development in the past and their distribution in the present, is almost overwhelming in its grandeur and its beauty. Almost all such loving students of

nature have found in the theory of Darwin, in his many stimulating works and in those of his friends and followers, the only intelligible clue to the mighty labyrinth of nature. To such students of nature the claims of the Mutationists and the Mendelians, as made by many of their ill-informed supporters, are ludicrous in their exaggeration and total misapprehension of the problem they profess to have solved. To set upon a pinnacle this mere side issue of biological research, as if it comprised within itself all the phenomena and problems presented by the organic cosmos, is calculated to bring ridicule upon what, in its place, may be an interesting and perhaps useful line of study. To myself, these monstrous claims suggest a comparison with those of the perhaps equally enthusiastic and equally ill-informed admirers of the immortal Pickwick, who believed his 'Speculations on the Source of the Hampstead ponds, with some Observations on the Theory of Tittlebats,' to have been a most important contribution to the Science of that period."*

Truly this is Ercles' vein. We cannot help feeling that in his solicitous care for the old bottles our critic has otherwise disposed of the new wine, and we fear that it has sadly disagreed with him.

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* *Contemporary Review,* August, 1908.

Still, when all allowances are made for this, as well as for the claims of sentiment and rhetoric, there is evidently some difference of opinion between Dr. Wallace and the Mendelians. To the nature of this difference we propose to devote a few paragraphs.

We shall assume that by Darwinism he understands the doctrine to be found under that heading in most elementary text-books, no doubt largely based upon his own well-known volume dealing with the subject. There is a principle of variability in virtue of which organisms tend to differ from their parents, and a principle of heredity in virtue of which they tend to resemble them. Given a struggle for existence induced by overproduction, we are led to the conception of a process of natural selection whereby the various forms of life might gradually evolve from one configuration or species to another. Such are the essentials of a theory which, whatever the measure of our belief, charms alike by its coherence and simplicity, and by the memory of the great man whose name it bears. Through natural selection it offered the first acceptable explanation of the way in which one species might pass into another, but it involves certain conceptions as to the nature of the organism. It assumes, first of all, a continuity in variability such that small and almost imperceptible variations may be accumulated until

they attain to the rank of specific distinctions. Secondly, we must suppose that these tiny variations are definitely transmitted from parent to offspring. We are led to regard the species as endowed with a plasticity through which, by the operation of natural selection, it can be moulded to its own advantage in this direction or in that. Nor does it appear that there need be any limits to the changes which a part or organ may undergo provided that the good of the species is not interfered with.

At the time when the workings of heredity were not understood these views passed current. When offspring did not resemble their parents the "Law of Reversion" was invoked and all was well. But with the advent of the Mendelian principle of segregation the position underwent a radical change. Reversion was soon seen to be only a special case of a general phenomenon common to the animal and vegetable worlds, and falls into its place in the orderly scheme of modern heredity. How the Mendelian discoveries bear upon the older conceptions of heredity and variation may perhaps be best illustrated by a simple example, and, as Dr. Wallace seems to view anything domesticated with mistrust, our example shall be a wild one. In the common white *Lychnis* (*L. vespertina*), the leaves and stems are usually covered with hairs. Sometimes, however, a variety is met with in which the

leaves and stems are quite smooth or glabrous. A cross between the hairy and the glabrous results in hairy plants alone. But when the hybrids are mated together the next generation consists of hairy and glabrous in the proportion of 3 :1. And these glabrous plants of hairy parentage subsequently breed true to the glabrous character. Hairiness and glabrousness form an alternative pair of characters, and as such are transmitted in the ordinary Mendelian way. Crossing results in no long series of intermediate conditions, but the two characters split cleanly from one another.

Now, on the theory which Dr. Wallace favours, it must be supposed that one of these forms came from the other by a very gradual process. For the sake of argument, we will suppose that the glabrous form arose from the hairy. We must imagine that this has happened by the gradual loss of hairs, and that if we had all the stages before us they would form a continuous series of diminishing hairiness, with the extreme hairy form at the one end and the fully glabrous at the other. And in order that the process may work, we must assume that the glabrous condition is of advantage to its possessor; otherwise natural selection would not act. Now to this conception of the evolutionary process the Mendelian humbly begs leave of Dr. Wallace to offer two criticisms. In the first place, why are the glabrous and the hairy forms to be found grow-

ing side by side, without the existence of intermediates? For *Lychnis* is a plant with separate sexes, and is freely crossed in nature by insects upon which its fertilisation depends. If the one form has been produced by the agency of natural selection, because it is of advantage to the species, why has the other not been selected out of being? Secondly, we ask why the commingling of the germinal material of the two forms effected by a cross does not eventually result in the production of a complete series of intermediate forms. Whence comes this element of stability into our supposedly fluctuating material?

Let us now take another instance. Dr. Wallace has quoted in support of his views certain opinions from a memoir* by Mr. W. L. Tower, of Chicago University. We, for our part, propose to give the reader a few of Mr. Tower's facts. The little beetle *Leptinotarsa decemlineata*, the dreaded "potato-bug" of North America, is known to present certain well-marked variations in nature. One of these varieties has from its lighter colour been termed *pallida*, and in Tower's opinion it fully holds its own with *decemlineata* under natural conditions. Tower collected and bred from some of these wild *pallida*, and found that they

* Carnegie Institution of Washington, Publication No. 48.

came true to type. He then crossed *pallida* with *decemlineata*, and concluded from the result of his experiments that "*decemlineata* is the dominant member of the cross in the hybrid generation, but in the succeeding generation we get a Mendelian separation." So far the case of the beetle is similar to that of *Lychnis*. Now comes the most fascinating part of Tower's story. He took a pure strain of *decemlineata* and subjected it to abnormal conditions of heat and moisture at the time when the germ cells of the little beetle were maturing. Certain individuals so treated were bred from, and the majority of their offspring were of the variety *pallida* nor were there any intermediates between the variety and the normal form. Tower infers, and the inference seems inevitable, that the variation from *decemlineata* to *pallida* was directly induced by the change of conditions to which the germ cells were exposed at a critical period. Now what relation does this artificially produced *pallida* bear to the *pallida* that is found in nature? Tower showed that there is every reason to suppose that they are one and the same thing. The artificial *pallida*, like the natural, bred true to its own kind, while when crossed with the normal form it behaved as a recessive and gave an ordinary Mendelian result in precisely the same way as the natural variety had been shown to do. It is difficult to imagine how

even the most bigoted of critics can quarrel with the inference that the natural *pallida* came as a sudden step or mutation, owing to the action of changed conditions upon the normal form. For why, asks the Mendelian, are we bound to assume gratuitously the existence of a series of intermediates which have never been seen, in order to bolster up a hypothesis for which no unequivocal experimental evidence has ever been produced? And with this question we may take our leave of Dr. Wallace and turn for a moment to Professor Poulton.

If the vein of Dr. Wallace is a tyrant's vein, Professor Poulton, though assuredly no lover, is more condoning. He recognizes that Mendel's discovery is not devoid of interest, and even proclaims a mild sympathy with the Mendelian school. His main criticism is of a somewhat different order to that which scientific men are accustomed to encounter, and, for our part, we confess that for a time we felt a little dubious as to the way in which it should be met. Mature consideration has, however, convinced us that it is of the order which demands a soft answer rather than any parade of facts. Professor Poulton tells us that the Mendelian writings are "injurious to Biological Science, and a hindrance in the attempt to solve the problem of evolution for the following reasons" (here follow six reasons neatly classified by num-

ber, from which we select the last two as containing, in our opinion, the pith of the argument):—

"5. The contemptuous depreciation of other lines of investigation directly inspired by the work and teaching of Darwin and Wallace.

"6. The natural consequence of this last:—a widespread belief among the ill-informed that the teachings of the founders of modern biology are abandoned."*

Moreover, Professor Poulton goes on to say that he has submitted his six reasons to a number of eminent zoologists, and that they have expressed their approval of his indictment. The Sacred College has been convened and orthodoxy has spoken through its chosen mouthpiece. We are in some doubt as to whether it is the greater or the lesser excommunication which has thus been pronounced upon us, but we hope that it is not yet too late for us to make our peace. Let us then hasten to assure Professor Poulton that if we have sinned it is not with our good-will. Our only business is with the discovery of truth, and we would not for one moment have it thought that we are competing for the patronage of the ill-informed. We trust that he will recognise the sincerity of our protestation, even if he continue

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* *Essays on Evolution*, Oxford, 1908.

to carry out his teaching as though the Mendelian school of heredity did not exist.

In conclusion, a few words upon the attitude of the Mendelians towards the problems of evolution. They are charged by Dr. Wallace with "a total misapprehension of the problem they profess to have solved." By this we take it he means the problem to which he himself preaches the only true solution—the great problem of the origin of species. Those conversant with the writings of the Mendelians will have little difficulty in absolving them from "these monstrous claims.'" To profess to have solved a problem and to suggest that in the light of new facts the old solution must be reconsidered are two very different things. The outburst of experimental work following upon the discovery of Mendel's paper has already resulted in a large and coherent body of new facts which cannot be reconciled with the old view of continuity in heritable variation. To be of any moment in evolutionary change it is necessary that variations should be inherited. Recent research has shown conclusively that discontinuous variations, presumably mutations, are transmitted according to a definite and orderly scheme, while no clear and unequivocal evidence for the inheritance of small fluctuating variations resulting in a stable change of form has hitherto been adduced. The inference, so far as we can draw one, is that

the specific differences which divide species from species have arisen by some mutational process rather than by the accumulation of minute and almost imperceptible differences. Which of these mutational forms persists and which disappears may well be decided by natural selection. "Natural selection," writes Bateson, "is a true phenomenon, but its function is to select." Its concern is with the survival and not with the origin of species. To hope to solve that problem we must know more—much more—of the meaning of sterility and of the physiological constitution of the living thing. That the experimental method offers the fairest hope of gaining such knowledge we are convinced. And if the results may lead us to reject the conclusions of those who have gone before, we may feel consolation in the reflection that the best disciples are those who heed the practice rather than the words of the Master.

R. C. PUNNETT.

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